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COMPARATIVE ANATOMY

OF THE

PHANEROGAMS AND FERNS

DE BARY

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COMPARATIVE ANATOMY

OF THE

VEGETATIVE ORGANS

OF THE

PHANEROGAMS AND FERNS

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WITH TWO HUNDRED AND FORTY-ONE WOODCUTS

AND AN INDEX

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TRANSLATORS' PREFACE.

In producing an English translation of the Comparative Anatomy of the Phanerogams and Ferns, by Professor De Bary, an attempt has been made to meet two requirements, which have long been felt. In the first place, those English students who do not read German will now gain access to the most exhaustive work hitherto published on that subject. Though, through unavoidable circumstances, a considerable interval has elapsed between the publication of the original and that of the translation, the book deals so largely with established facts, and in so much less a degree with matters of controversy, that the delay affects its value but little. The Translators have however inserted references to the more important memoirs published since the original was produced.

In the second place, by means of this translation it is hoped that suitable English equivalents will have been supplied for numerous technical terms which have not hitherto been translated. Thus, in that part of the book which deals with the arrangement of the vascular bundles (pp. 232–315), the introduction of new English terms has been especially necessary, since this part of the science has not hitherto been treated at length in any English text-book.

In conclusion, the Translators wish to record their thanks to Mr. W. T. Thiselton Dyer, Assistant Director of the Royal Gardens, Kew, and to Dr. S. H. Vines, Fellow and Lecturer of Christ's College, Cambridge, for valuable advice and assistance; also to Mr. W. B. Hemsley, for the good judgment and care with which he has prepared the index.

April 22, 1884.

TO THE READERS.

The present volume will complete the Handbook of Physiological Botany, which, since its commencement in 1865, has been edited by the late Prof. Hofmeister. As stated in the Preface to Vol. I, the plan of the book was drawn up in the year 1861, and the sections, which were to be treated according to the state of the science at that time, were distributed into four volumes, and among six contributors. Arrangements were made beforehand, so that the Volumes might be expected to appear in quick succession. Two of the contributors retired at the outset, so that, in the year 1866, the fourth volume having first appeared, and then the first section of the second, the programme in the Preface of Vol. I. assigned all the volumes to four contributors, and those still remaining to three. Of these another subsequently retired. Nevertheless, the undertaking was not given up, the preparation of the remaining parts being undertaken by Hofmeister and by the author of this volume.

At the beginning of last year Hofmeister was attacked by severe illness, to which he succumbed on the 12th of January of this year. After his death the question of the fate of the Handbook presented itself to the surviving contributors. Among the papers of the deceased were found, it is true, drafts and beginnings of the parts he had undertaken. But they have so much the character of incomplete sketches and fragments, that it was obvious to the undersigned that their publication would neither answer the purpose of the Handbook, nor the intentions of their author. The case standing thus, the remaining parts would have to be undertaken by another contributor. Supposing some one to be ready at once, he would have to begin on his own account at the beginning, and the continuation of the Handbook would at best be delayed for years. Nevertheless, if there were a real want, the attempt to continue it would be made. But, in the sixteen years which have passed since the Handbook was planned, the position of our Science has altered. In face of the Literature of to-day, a new work comprising 'the Morphology of the Vascular Cryptogams,' and 'the Sexual Reproduction of the Phanerogams,' can be dispensed with, while a separate treatment of the 'Algæ,' as at first intended, is hardly possible. On these grounds it has been determined to close the Handbook. As it stands at present, it is arranged as follows:—

Vol. I. 1st Part. 'Die Lehre von der Pflanzenzelle.' By W. Hofmeister.
2nd Part. 'Allgemeine Morphologie der Gewächse.' By the same author.

Vol. II. 'Morphologie und Physiologie der Pilze, Flechten und Myxomyceten.' By A. de Bary.

Vol. III. 'Vergleichende Anatomie der Vegetationsorgane der Gefässpflanzen.' By the same author.

Vol. IV. 'Experimentalphysiologie der Pflanzen.' By Julius Sachs.

A. DE BARY. J. SACHS.

Strassburg and Würzburg, *June*, 1877.

PREFACE.

The preparation of the present volume was begun by the author in the year 1865, after the other contributors to the Handbook, who had originally undertaken it, had retired. It was fairly far advanced, when in 1867, by reason of other necessary business, it had to be put entirely on one side for almost two years. It also suffered frequent and long interruption at a later time through changes in the official engagements of the author.

The object of the work, as stated in the programme of the Handbook, was an epitome of the present knowledge of 'the Anatomy of the Vegetative Organs of Vascular Plants.' From the very first, the necessity of numerous confirmatory investigations was apparent, since the descriptions at hand were written at very different times, and by very different authors, and it was only possible to judge of and sift the differences necessarily present in these by actual and personal observation. This led to many researches of my own: new results and new questions appeared. The work soon extended itself beyond the limits originally intended. When one section was successfully finished, and others were in hand, new publications appeared which demanded fresh alteration of what had already been done. Therefore, in order that at least something might result, the necessity finally arose of bringing this work of the Danaids, this supplementary patching and correcting, to a definite conclusion, and of finally closing the work. This was done about three years ago. Since then nothing of importance has been done beyond finishing the revision.

That such was the progress of the work may be some explanation and excuse for the frequent unevenness of the performance. Further, the, so to speak, forced hurry of the conclusion necessarily imposed limits. With regard to the contents, the exclusion in the first place of all Palæontology and Pathology, the latter including the phenomena of wounding and healing by Callus, &c., is understood. Also the small sections on the throwing off and fall of the Leaf, &c. were omitted as of minor importance. Further, it was unavoidable that the use of the newest Literature should be limited. Much that has appeared in latter years has, to my sorrow, been consciously and intentionally left unused. On the ground of the above explanations, I particularly beg to be excused for this.

From the older Literature I have perhaps cited too much for many, and for others too little. But here also arose the necessity of keeping a definite limit, in order to bring something to completion. On the anatomy of plants such an indescribable amount has been written, that, in a comprehensive treatise, one or many authors might be cited in reference to every word. To carry this through, even to the extent to which it is done in the section on Epidermis, makes the

description exceed the bounds of convenience and overstep the limit of human power and endurance. I have therefore placed a check upon this also, and, once for all, I will say in answer to possible claims, that every word in this book has had a previous author, printer, and publisher. I hope that I have as a rule referred sufficiently to fundamental works: still it may be emphatically stated that the chief sources and foundations of my work were the writings of Mohl, Nägeli, Sanio, Th. Hartig, and in the latest times of van Tieghem, although in some cases I may have omitted to cite them expressly. I presuppose a knowledge of the Text-book of Sachs. When this is quoted, and no further information is given, the fourth edition is always meant.

The old Literature is only cited when absolutely necessary, since it lies outside the purpose before us, to write a history of the anatomy of plants. In *Sachs*' History of Botany, *Treviranus*' Physiology, and *Meyen's* Phytotomy and System of Vegetable Physiology, the reader will find what is wanting here.

The plan and course of description are more exactly indicated in the Introduction. The book deals in the first place with the *actual mature structure* of the higher plants, and touches upon the history of development only by way of assistance. We do not thereby ignore the fact that the description of the mature condition must necessarily be based upon the history of development, since that which is termed mature is nothing more than a further advanced part of the whole course of development of the individual. It must therefore always be referred as a matter of course to earlier stages of development, and be coupled with them. But it was the more the object of this work to put that stage of development which is called mature to the fore, since the present overruling preference for the earlier stages has often brought it about that in the 'voir venir,' the things themselves, which are to be produced, are neglected.

I know only too well how far the book falls short of the object indicated in the title. The name 'Vorarbeiten,' or 'Prodromus,' of a comparative anatomy would better correspond to the result. That title was only rejected for shortness, sake, and on the consideration that every work should be the predecessor of a better.

Most of the figures were drawn by the author on wood, from nature. In case of those copied and borrowed from other books the source is given in each case. I am specially thankful to my respected colleague *Sachs* for the permission to use the woodcuts of his Text-book, and I should have made still further use of them had not a number of the figures here given been already cut before the earlier editions of the Text-book appeared. I may offer this expression of thanks without presumption not only in the name of the author, but also in that of the reader. Also in the name of both I may add thanks to Dr. von Rostafinsky of Krakau, who has constructed the index of names.

A. DE BARY.

STRASSBURG, *June* 15, 1877.

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INTRODUCTION.

The body of the plant is composed of parts with definite position, succession, structure, and direction of growth. These we call its *members*[1], when we refer only to their share in the structure. Investigation teaches us to recognise members of different, and, in plants of complicated structure, numerous ranks. Roots and leafy shoots; internodes, leaves, segments, and layers of meristem, masses of cells; finally, the single cell, which may again be separated into members.

Each member, of whatever rank, is adapted according to its development to definite physiological work. It becomes the instrument, or *organ* of this work. As was the case with members, there may also be distinguished organs of different rank—simpler, and gradually more complicated. According as an organ adapts itself to a definite function, it attains properties of form and structure, which are definite, and differ from those of other organs.

The description and explanation of the collective phenomena of form and structure constitute the task of morphology. According to the two points of view now put forward, we must distinguish between the morphology of members, and the morphology of organs. The former deals exclusively with the phenomena and laws, according to which the organism is compounded of the members of different rank; the morphology of organs with the properties of structure and form, by which the members become organs, and with the distinction of organs of different rank, according to those properties. Strictly speaking, the morphology of the organ presupposes a knowledge of that of the member, since the origination of a member must precede its evolution into an organ. As a matter of fact, a sharp separation of the two disciplines can hardly be carried out, since both work with the same material, which extends from the realm of the one to that of the other without any definite break.

The subject of this book is a part of the morphology of the organs of Plants, which is limited for convenience sake. According to the programme of the Handbook, of which it is a part, it should treat of '*the anatomy of the Vegetative Organs of Vascular plants*;' it is occupied therefore only with the Phanerogams, and Pteridophyta, i. e. the Fern-like plants in the widest sense of the word. Further, it presupposes such knowledge, gained from other sources, of the outward form of organs of higher rank (e. g. foliage-shoots, roots, &c.) as can be acquired without anatomical investigation, and treats only of their internal structure. Lastly, it is limited to the

[1] Sachs, Textbook, second English edition, p. 149.

vegetative organs. Having regard to the points of view established above, as well as to considerations of the available space, the work has further to presuppose a knowledge of the morphology of members—otherwise called the general morphology of plants, and general doctrine of the cell—and only to touch on these subjects as far as may be necessary.

Since the investigation extends over three great sections of the vegetable kingdom, it will be our task to describe comparatively those phenomena, in which the representatives of these sections correspond, or differ: that is, to offer a *comparative anatomy* of the vegetative organs.

Under the term vegetative organs we include all those organs of the plant which are not organs of reproduction, i.e. which do not, sexually or asexually, serve in the production or direct preparation of germs: the term includes therefore those organs which undertake the entire work of preservation of the physiological individual, and which may take different parts in this work.

In the plants in question, which always have members of many grades, those of every sort and rank are to be found developed into vegetative organs: both those belonging to the highest ranks, which are externally apparent, such as roots, leafy shoots, with their internodes and leaves; and of successively lower ranks, such as definite groups of cells, and lastly single cells, or the products of their metamorphosis. But investigation shows that the adaptation to, and participation in vegetative duties, that is, the development into organs of definite function, and corresponding structure, is far the most commonly and definitely carried out for members of lower ranks, i.e. for cells, and groups of cells, or the products of their metamorphosis. It is these which in the first instance share among them the vegetative work, and assume a correspondingly characteristic form and special structure. A member of higher rank composed of them is only a vegetative organ of higher rank, inasmuch as it consists of them. The structure characteristic of such an organ is determined by the structure and distribution of the organs of lower rank, which compose it. The vegetative structure in question is not universally connected with definite members of higher rank. Equivalent members, it is true, very often develope into equivalent organs: the functions of the leaf, assimilation of carbon, transpiration, &c. are, for instance, usually deputed to leaves: most roots are equivalent to one another in both relations. But, on the other hand, the converse is not uncommon, that non-equivalent members are equivalent organs. In many plants besides the leaves the internodes also, which are connected with them, take part in the functions of the leaf: in others, with 'leaf-like' stems, the function and corresponding structure, which the leaves have lost, are transferred to the stems. Trapa natans has part of the petiole developed into a swimming organ: in the floating species of Desmanthus internodes of the stem, and in species of Jussiæa certain roots assume this function, and corresponding structure.

This being the case, the description of the structure of the vegetative organs must start from the consideration of simpler forms, i.e. the cells. Since the investigation of these separately is necessarily followed by that of their connection with others, and of their arrangement into tissues of various grades, the structure of the organs composed of these gradually becomes apparent.

Those cells or their derivatives, which have the character of definite vegetative organs, seldom occur, in the plants in question, singly between dissimilar ones;

usually similar cells are connected so as to form large groups or masses. An aggregation of cells growing in common is termed generally a *Tissue* (Tela, contextus; in compound words ἱστίον[1]). Each tissue, which is characterised by definite properties, and distinguished from others, is called a *tissue-form* or, better, a *sort of tissue*. For the single cells which belong to a tissue, or for each elemental form derived from such a cell, the term *tissue-element* may be reserved. Tissue-elements which occur singly between dissimilar ones (Idioblasts, after Sachs' terminology) usually correspond in their properties with others which occur in connection with similar elements. They are then to be reckoned as of the same sort of tissue as the latter. In like manner, finally, such tissue-elements as occur only as Idioblasts (for instance many laticiferous tubes) will form together with one another a special sort of tissue. All tissue-elements, which correspond in definite similar properties, are therefore termed collectively a sort of tissue, whether they be Idioblasts, or are connected with like elements.

The course of description which is followed in this book may be gathered from what has been said. The first subject is the characterising and distinguishing of the sorts of tissue, which serve as vegetative organs; then the grouping and arrangement of these in building up the members or organs of higher rank. In this course of description a difficulty certainly arises: this can only be overcome by the establishment of a limit, which is to a certain extent artificial. Those tissues, which act functionally as vegetative organs, are often continuous in the plants in question with those higher members, which are according to their most important adaptation reproductive organs. The member of many Ferns which acts functionally as a Prothallium is principally composed of chlorophyll-containing Parenchyma, similar to that of foliage leaves. This sort of tissue, together with vessels, vascular bundles, &c., takes part in the construction of the parts of the flower of many Phanerogams, &c. Many peculiarities of vegetative tissue, which appear in these parts, depend much less, it is true, on the properties of the single tissue-elements, than on their arrangement. Since these peculiarities are directly connected with adaptation to the generative process, the study of them should also be in connection with it, and must be excluded from this treatise. In cases of sharply-defined phases of development, the boundary, which must needs be drawn, is evident at first sight. For instance, no one will expect the Fern-Prothallium to be treated of here. But among the Phanerogams there often occurs a gradual transition between purely vegetative and reproductive organs. To satisfy in the present case the necessity of a definite limit to the subject in question, all that falls under the definition of flowers, specialised inflorescences, or parts of inflorescences, will be excluded from consideration.

As has been already intimated, the differentiation of the sorts of tissue is a phenomenon which accompanies the development of a part to maturity. Originally the cells of a part differ, it is true, in certain relations, both in form and direction of division; but they correspond in structure, and in the fact that, while they increase slowly in size, they divide repeatedly; and thus finally produce cells, which develope into tissue-elements. From those phenomena of division, such masses of cells are termed *Meristem*; and when they form the first foundation of a member *primary*

[1] Compare Unger, Anatomie, p. 138; Sachs, Textbook, English edition, p. 70.

meristem[1]. In structure the cells of meristem are characterised by having a delicate homogeneous membrane (only in certain exceptional cases thickened and with flattened pits), and homogeneous, finely granular protoplasm with a nucleus, but with no further recognisable structural elements. By reason of their constant division, they are throughout in uninterrupted connection with one another.

In each system of the meristem the divisions pass through a definite number of stages, till they gradually cease. According as this happens, the cells, first formed as members of the meristem, assume those properties, by which the further sorts of tissue are distinguished: great increase in volume takes place, and changes of structure and form; while the latter may result in a partial loosening of the original uninterrupted connection, i.e. in the appearance of *intercellular spaces*.

As compared with the meristem, the tissue elements derived from it attain a great constancy both of form and structure. They have accordingly been termed *permanent tissue*, *fixed tissue*, or mature tissue. If the idea of tissue be understood in the general sense stated above, the meristem also is naturally included: we distinguish then on the one hand meristem, or formative tissue, on the other permanent tissue, as the two main categories of tissue. Merely for shortness of expression, however, the term tissue will be used also for permanent tissue in opposition to meristem. In this sense, and according to the previous explanation, the following pages will deal with the *vegetative tissues*, which serve as vegetative organs.

Comparative investigation shows that the cells of the meristem universally correspond very closely in the general character of their structure, and the same may be said of the main phenomena of the vegetative process in the plants we are engaged with. Answering to this correspondence of origin and functional adaptation, the forms of tissue in the whole group on which we are engaged correspond in their main properties, notwithstanding frequent modifications to suit special cases, and the same few tissue-forms everywhere occur.

Tissue-elements of every sort are derived from the cells of the meristem, each has originally the properties of a cell. Accompanying definite development there first appears the fundamental difference, that certain elements *retain* during their life the structure and all the characteristic properties of typical cells, others *lose* the cell nature. The former are composed of a completely closed cell-membrane and active protoplasm, with a nucleus and cell contents; they retain the power of independent growth, and remain capable of division; in consequence of this property a meristem may again arise from them, and this, in antithesis to the original, is distinguished as *secondary meristem* (Nägeli, l.c.). The latter lose with their development the power of division, and of independent growth; usually they cease entirely to grow, but in many cases a real lasting growth of such elements occurs, resulting from their nourishment by adjoining cells. In their structure, the loss of the cell-nature is indicated either by the complete disappearance of the protoplasmic body, its place being filled by other bodies, usually air or fluids; or by its suffering characteristic changes, which vary according to the individual cases. The latter observation is made with special

[1] Nägeli, Beiträge, I. p. 2.—Schleiden (Grundz. 3 Aufl. I. p. 253) and Karsten (Veg. Org. d. Palmen) include these masses under the wide term *Cambium*; Unger (Anat. und Physiol. p. 180) calls them formative cells: Schacht (Pflanzenzelle, p. 165) primary parenchyma.

reference to the sieve-tubes; it remains doubtful whether the contents of these are protoplasm or not. The cell-walls of the elements in question are wholly or mostly retained.

According to the differences already mentioned, which will be further followed out in the subsequent special observations, the tissues divide themselves into those which consist permanently of cells (cellulæ), and those whose elements are descendants, derivatives, or products of change or *metamorphosis* of cell. According to their form and other properties these are termed *tubes* (Tubi, Tubuli), *vats* (Utriculi), *fibres* (Fibræ), and are distinguished from cells.

Most tissue-elements, of whatever sort, are formed directly and quickly by the metamorphosis of meristematic cells. Exceptions from this rule only occur in certain cases when cells, after they have acted as such for a long time—even for years—may secondarily pass over to another tissue-form. This takes place in the secondary development of Sclerenchyma, which will be described in chapters II. and XV.

From this *secondary metamorphosis of tissue* we must distinguish *death*, and the changes eventually connected with it, which appear in certain other cases in the tissues, such as the dying off of old hairs, cork cells, cells of the pith of many plants, of the elements of bark, and of the old wood of Dicotyledons, &c.; appearances which can usually be distinguished with ease from metamorphosis of tissue by the commencement of rotting, weathering, &c.

In accordance with the preceding considerations, the distinction of the forms of tissue which act as vegetative organs, and the classification of the study of them, must in the first place be founded upon their structure, that is, on the structure of the single tissue-elements, and the connection of these with one another—whether they be connected with like or with unlike elements. It is obvious that, in organized bodies, certain peculiarities and varieties of structure are connected with certain phenomena of development. And it is not less obvious that varieties of structure are also as a rule correlated with certain varieties of form of single tissue-elements. But experience teaches that between form and structure a *constant* relation does not exist, or at least not universally; and that, contrary to the older classifications, which regarded in the first place the form of the elements, this is of only secondary importance in the distinction of the tissues.

According to the principles now laid down, the following main forms of vegetative tissue may first be distinguished:—

I. *Cellular tissue*, i.e. that which consists of permanent typical cells; with the main subdivisions, *epidermis*, *cork*, *parenchyma*. II. *Sclerenchyma*. III. *Secretory structures*. IV. *Vessels*. V. *Sieve-tubes*. VI. *Milk-tubes*. Separate notice of the *Intercellular spaces* may, with advantage, though perhaps not necessarily, be appended to the study of the tissues.

The study merely of the divisions and subdivisions of tissue form is at all points closely connected with the arrangement of these into combinations of different rank—so as to form vegetative organs of successively higher rank—so far so, that the two modes of study can never be completely separated the one from the other.

According to their form the combinations of any rank may be distinguished as *Layers*, *Bundles*, *Masses* (*Groups*, *Nests*)—terms, the meaning of which is obvious from

the ordinary use of the words: a sharper definition of them is here neither necessary nor possible. When a layer (simple or compound) surrounds a tissue, which differs from it, it is termed relatively to the latter a *sheath*. Tissues of whatever sort or rank may be mutually continuous for long distances, or throughout the whole plant. When this is the case, they are said collectively to form a *System*. A system of any rank may be composed of systems of lower rank, or may join with others to form a system of higher rank. For instance, the Vascular system is composed in most plants of that of sieve-tubes, and that of vessels; each of the latter is a system of itself; the two combine as a rule to form the above-named system of higher rank; while often the system of Sclerenchyma-fibres joins them as a third constituent of the joint system.

According to the point of view from which one starts, one may therefore distinguish systems in the most various sense, as will appear in the later chapters; for instance, in the Dicotyledonous stem we may with equal right distinguish a Vascular and an Epidermal system, or a Woody and Cortical system, whereas the latter includes, besides the Epidermal tissue, a part of the Vascular system, and other tissues besides.

Sachs (Textbook, Eng. ed. 1882, p. 79, etc.), in the exposition of the anatomy of the higher plants, starts from the definition of three systems of tissue, which he terms Dermal, Fascicular, and Fundamental tissue. Under the first term he includes those tissue-forms, which limit externally such plants as have their cells aggregated in three dimensions of space, as a matter of fact, Epidermis and Periderm (cf. § 2, 23 and chap. xv). His Fascicular tissue corresponds in the main to the previously mentioned Vascular system (chap. viii). The name Fundamental tissue includes what remains after the separation of the other two. However much this distinction may be fitted to guide beginners, still, in my opinion, it does not answer its purpose, which is to serve as a basis for a uniform exposition of the various differentiation of plant-tissues. For the names Dermal and Fascicular tissue indicate in Vascular plants systems of tissue, which are positively characterised by definite tissue-forms: but the name Fundamental tissue implies the remainder, and this may just as much consist of different positively characterised tissue-forms, and tissue-systems, which are equivalent to the Dermal and Fascicular systems. But if it is necessary, in the description of the Dermal and Fascicular systems, to make use of a short general term for the tissues over and above these, the terms Fundamental tissue, or Fundamental mass, or Intercalary mass, are very suitable; just as in Nägeli's treatise on the vascular bundles, or fibro-vascular masses, was his distinction of these from the rest ('Proten'), or as was Schwendener's general term for the parts of the vascular bundle, which, in his exposition of the mechanical adaptation, did not bear upon his point. And indeed in describing a form or system of whatever rank, some such method must always be used. I think, however, that the distinction of the forms of tissue must first serve as a foundation for the uniform exposition of the subject which now engages us, and for the choice of terms; then only should follow the investigation, how far these forms of tissue take part in the formation of combinations, and systems of higher rank.

Although on the one hand the course of exposition above brought forward has a definite justification in all cases, and, on grounds which need not be repeated, will be in the present case pursued, and although further the distinction of single forms of tissue must be carried out under all circumstances with regard to the structure of the elements only, still the question arises, on the other hand, if the distinction of definite systems could not be drawn more naturally on other than the purely histological grounds above stated; that is, on such as are derived from the morphology

of differentiation (i.e. the history of development). Investigation has taught that the original meristem, from its first (embryonic) beginning onwards, maintains a well defined differentiation into different—but always meristematic—layers, or segments; and that, in the plants on which we are engaged, in many cases definite sharply marked masses of tissue (I may mention provisionally the axile vascular bundles of many roots) are derived from certain of these layers, others from other layers, just as the different tissue-systems of the animal body are derived from the different germinal layers. The question may therefore arise whether, over and above the distinction of forms of tissue according to definite structure, the exposition of the tissue-systems, and of the construction of the members of the highest rank from them, must not refer to that differentiation of meristem, and take it as the foundation. The determination on this point will depend upon the answer of the further question, whether the origin of each, or of single tissues or tissue-systems, from one and the same portion of the primary meristem, can or cannot be generally proved. For if the latter is the case, if parts of the same tissue-system originate from unlike parts of the meristem, the course of exposition which we are considering must be put aside as impracticable.

In order to gain clearness on this question, a survey of the original modes of differentiation of meristems is necessary; and though this lies beyond the strict limits of the subject of this book, still it may with the more reason be here inserted, since in the following chapters reference must constantly be made to that differentiation [1].

I. As Hanstein [2] has shown, the young embryo of the *Angiospermous Phanerogams* separates, while still consisting of few cells, all of which are meristematic, into three layers, or groups of cells, which differ in their arrangement and direction of division; these were termed by their discoverer, Dermatogen, Periblem, and Plerome [3]. At the end of the root there is besides these a fourth, the origin of which in the embryo remains to be further investigated. This was called by Janczewski [4] the Calyptrogen layer: we shall return to this later. The dermatogen layer is separated by a single tangential division of the few cells, which form the original rudiment of the embryo, as a simple peripheral layer of cells. It remains a simple layer of cells, since all the subsequent meristematic divisions which occur in it take place only by walls at right angles to the surface. It is only at the future apex of the root that other phenomena appear, which need not be more fully discussed at present. Further divisions of the cells enclosed by the dermatogen separate an axile longitudinal cylinder, the plerome, from the periblem, which is a zone of tissue lying between the plerome and dermatogen. The plerome consists of cells in which longitudinal divisions preponderate, and which have a corresponding arrangement; the periblem of cells distinguished from the former by more frequent and irregular transverse divisions.

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[1] [See further Sachs, Ueber die Anordnung d. Zellen in d. jüngsten Pflanzentheilen, Arb. d. Bot. Inst. in Würzburg, Bd. II; also, Ueber Zellanordnung u. Wachsthum, ibid.—Haberlandt, Scheitelzellwachsthum b. d. Phanerogamen, Botan. Zeitg. 1882, p. 343.—Nägeli, Scheitelwachsthum d. Phanerogamen, Naturforscher Vers. zu München, 1877.]

[2] Hanstein, Botan. Abhandl. I. On the details of the origination of the embryo, and its great differences in those Di- and Monocotyledons which have been investigated, the reader must be referred to this treatise and to Sachs' Text-book, English edition, 1882, pp. 585–593. Further, Fleischer in Flora, 1874, p. 369, &c.; Hegelmaier, Bot. Zeitg. 1874, p. 631, &c.

[3] Hanstein, Die Scheitelzellgruppe im Vegetationspunkt der Phanerogamen, Bonn, 1868.

[4] Ann. Sci. Nat. 5 série, tom. XX.

This differentiation of the meristem is retained at the *punctum vegetationis* of the first stem and of the tap root; further it appears at the *punctum vegetationis* of all lateral stems and secondary roots. The differentiation certainly varies greatly in distinctness in different cases, and is complicated in roots by the presence of the Calyptrogen-layer. It corresponds exactly to the scheme given above in the apex of the stem of many thin-stemmed water plants, as *Elodea*, *Hippuris*, &c.; in these Sanio[1] first discovered the appearances in question, which were afterwards more fully worked out by Hanstein[2]. The rounded conical apex of the *punctum vegetationis* of Hippuris (Fig. 1) is covered by a single layer of dermatogen (*e*). Then, passing inwards, follow usually five regularly concentric layers of isodiametric cells, these constitute the periblem which surrounds the plerome-cylinder (*p–p*). The latter has a bluntly conical apex, where it is often terminated by a single cell, while below it widens out. In most other cases the number of periblem-layers is smaller, only 2–3.

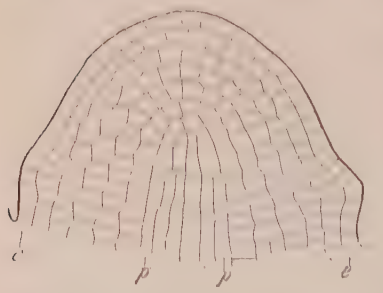

FIG. 1.—(225) *Hippuris vulgaris*. Median longitudinal section through the apex of quite a young leafy shoot, which had just begun to develope the second wheel of leaves. In older shoots the apex is much more elongated (cf. Sachs, Textbook, Engl. ed. 1882, p. 134). For further explanation see Text

The three zones of meristem, though they remain distinct, equally take part in the acropetal growth in length of the end of the stem. Each is continually renewed by divisions in the group of cells (or single cell) which forms their apical portion, while as the tissues are removed from the apex the transition from meristem to the definitive tissue takes place. Each is continuous downwards into definite tissues or tissue-systems, which will be mentioned hereafter. That apical group of cells, or (as in the plerome of Hippuris) single cell, which renews the layer and which hence always introduces the further cell-divisions in it, is called the *Initial cell* or *Initial group* of the layer.

In all Angiospermous plants the dermatogen layer is marked off with similar sharpness from the tissues below it, and is distinguished by its division walls being arranged only at right angles to the surface; with this restriction they run in all directions. But the separation of plerome and periblem does not appear in all cases so sharply marked as in the foregoing instance. Especially where the apex of the stem is broad and flat, it must often be left undecided whether both do not originate from a single common initial group, and are first clearly separated at some distance from the apex, on their gradual transition to definite systems of tissue.

The origination of the normal lateral branches of the end of the stem (i. e. of the leaves and lateral shoots) as emergences of the surface begins beneath the apex by the outgrowth of definite groups of meristem, which were not previously to be distinguished by any special character. These are the initial groups of the emergence. As a matter of fact, both elements of the dermatogen-layer and of the periblem lying under it take part in the origination, the growth and divisions of both proceeding simultaneously (comp. Fig. 1); but the cells belonging to the dermatogen

[1] Bot. Zeitg. 1864, p. 223.

[2] [Kny, Botan. Zeitg. 1878, p. 760.]

during all their further growth are divided only perpendicularly to the surface, so that the dermatogen-layer is continuous as a single layer also over the branches. The plerome-cylinder of the mother shoot, as far as investigation extends, takes no part in the origination of a branch. In the lateral shoots thus founded the separation of the meristematic mass, covered by dermatogen, into periblem and plerome first appears after some time. Both in this case originate from a common initial group, which is derived from the periblem of the mother shoot.

In the *punctum vegetationis* of the root of the Angiosperms[1] the same differentiation of the meristem often appears, as in the stem, but sometimes much more definitely. It should be described in the same terms as the latter, so far as the correspondence is exact. To the meristem, from which springs the body of the root, is added in all roots the conical cap, made up of layers of cells, which is known as the *Root-cap* (calyptra). This covers the meristematic *punctum vegetationis*, and is increased by it, according as the cells on its outer surface die off. Since this accession originates in certain cases from a special layer of meristem, the latter is, according to Janczewski, to be distinguished as the *calyptrogen*. As has already been said above, we cannot here discuss what genetic relation this bears in the main root of the embryo to the first meristem-cells of the hypocotyledonary stem. We must also take no notice here of the origination of the layers of meristem of lateral roots, our knowledge of which is for the most part due to Janczewski.

At the active *punctum vegetationis* of the roots of the Angiosperms, which has already begun to grow in length, four different cases of differentiation, which vary according to the species or groups, have been made known to us by Janczewski:

1. The meristem at the apex is differentiated into four sharply marked off layers: *plerome-cylinder*, *periblem*, *dermatogen*, and lastly the *calyptrogen-layer*, which covers the latter, and which soon disappears owing to the short duration of its activity. This differentiation is found only in two Monocotyledonous water-plants, viz. Hydrocharis and Pistia stratiotes[2] (Fig. 2).

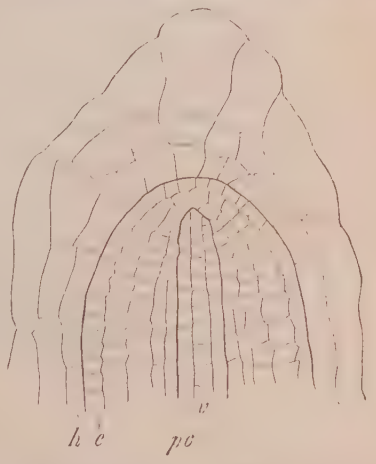

FIG. 2.—(450) *Pistia stratiotes*. Median longitudinal section through a young lateral root. *h* Root-cap, including calyptrogen-layer; *c* dermatogen; *pc* outer layer of the plerome-cylinder (pericambium); *v* foundation of an axile vessel in this. Between *c* and *pc* the periblem, which consists at the apex of only a single layer.

2. Sharply defined plerome-cylinder, and calyptrogen-layer. Between the two, at the apex of the *punctum vegetationis*, is an initial group only one layer of cells thick, which splits immediately behind the apex into periblem and dermatogen (i. e. cortex and epidermis). This is the case in most of the Monocotyledons which have been

[1] [See further Holle, Botan. Zeitg. 1876, p. 241; 1877, p. 537.—Eriksson, Botan. Zeitg. 1876, p. 641.—Schwendener, Scheitelwachsthum d. Phanerogamen-wurzeln, K. Acad. Wiss. Berlin. 1882; Botan. Zeitg. 1882, p. 687.—Flahault, Ann. Sci. Nat. sér. 6, Bot. tom. VI. pp. 1–229.]

[2] [Kubin, Hanstein's Abhandl. Bd. III. Heft 4, 1878.]

investigated; e. g. species of Allium, and Canna, Hordeum vulgare, Triticum vulgare, Zea Mais (Fig. 3), Stratiotes aloides, Alisma Plantago, Acorus Calamus, (Janczewski).

Treub[1], as the result of his extended researches, ascribes this differentiation to Juncaceæ, Hæmodoraceæ, Cannaceæ, Zingiberaceæ, Typha, Cyperaceæ, Gramineæ, Commelyneæ, Potameæ, Juncagineæ, Sagittaria, Limnocharis, Stratiotes. But he differs from Janczewski with regard to Allium, Acorus, and Alisma, since he does not allow the presence of a calyptrogen-layer in the families Liliaceæ, Asteliæ, Xerotideæ, Aspidistreæ, Ophiopogoneæ, Amaryllidaceæ, Hypoxideæ, Dioscoreæ, Taccaceæ, Bromeliaceæ, Musaceæ, Orchideæ, Palmæ, Pandaneæ, Cyclantheæ, Aroideæ except Pistia, further in

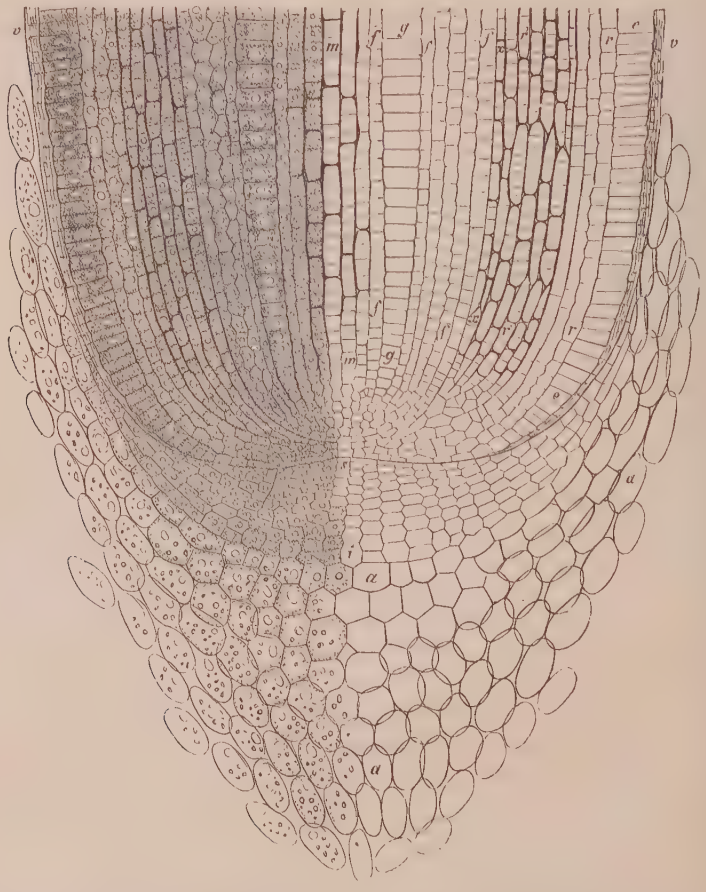

FIG. 3.—Median longitudinal section through the apex of the root of *Zea Mais*, from Sachs' Textbook. *a—a* outer, *i* inner layers of the root-cap; *s* calyptrogen layer; *m g f f'* plerome; *g* rudiment of a vessel; *x*, *v—r* periblem, or the cortex which has developed from it; *e* Epidermis, or dermatogen layer (*v* = the thickened outer wall of its cells). Above the apex of the plerome cylinder, easily seen between *m* and *s*, the dermatogen and periblem layers are reduced to two initial layers, which occupy the depressed centre. According to Janczewski the initial group should consist of a single layer.

the Iridaceæ, Pontederiaceæ, Sparganium, Butomus, and doubtfully in Alisma. He finds rather, covering the sharply defined apex of the plerome, a group of common initial cells two layers thick, from which originate root-cap, dermatogen, and periblem. Hence, the last named families should represent a special type, differing to a certain extent from those first named.

[1] M. Treub, Le méristème primitif de la racine dans les monocotylédones, Leiden, 1876.

3. (Fig. 4), Plerome-cylinder and periblem sharply defined, the latter overlying the apex of the plerome, and covered by a common initial layer for dermatogen and root-cap. The divisions of the initial layer, which are parallel to the surface of the bluntly conical apex, add on the one hand new cells to the root-cap above the apex, and on the other hand renew the initial layer itself. As the distance increases from the apex of the periblem, which by its growth in length is constantly advancing, the divisions become rarer, and at last cease. The last of these separates the initial cell into two, one of which is added to the root-cap, the other to the dermatogen as a permanent member of it. We may therefore say with Janczewski that root-cap and dermatogen arise in this case from the calyptrogen-layer. The cells of the dermatogen and root-cap, which owe their origin to the division just described, divide further by walls perpendicular to the surface; from each therefore is produced a section of a layer consisting of several or many cells. In the root-cap each of these sections is so arranged relatively to the similar ones laterally next it, and to others which have arisen above the apex, as to form a conical hood one layer of cells thick; and the whole root-cap is built up of such hoods fitting one into another. The cells of the sections of the dermatogen undergo extension perpendicularly to the surface, in such a measure that each section remains for a time considerably less extended in that direction than its predecessor, which is farther from the apex. The surface of the dermatogen layer therefore becomes narrower, as the apex is approached, by steps which occur at definite distances from it. Each step is covered by that section of a layer of root-cap which originally corresponded to it, while the edge of the latter abuts on the next lower, that is, the next older step.

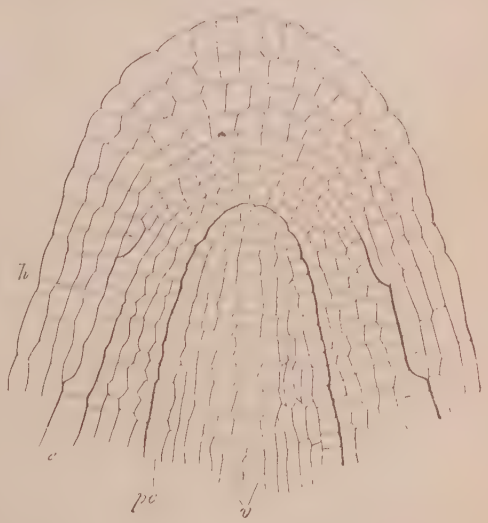

FIG. 4.—(270) *Polygonum Fagopyrum*. Apex of root in median longitudinal section. *p c* pericambium, the outer boundary of the plerome-cylinder; *e* dermatogen or epidermis, between *p c* and *e* periblem, *h* root-cap.

A not unimportant variety occurs, according to Janczewski, within the type of differentiation in question. In the majority of plants which have been investigated, the periblem consists at its apex of a single initial cell (Fig. 4) or of two such, which lie side by side in one layer; it is below the apex that it first increases to several layers. But in one case, namely, Linum usitatissimum, the apex of the periblem consists of two initial layers. One of these, the inner or lower of the two, behaves as in the first case just described. The other, the outer one, belongs to a layer of cells, which clothes the whole periblem. This, like the dermatogen, divides only perpendicular to the surface, and therefore always remains a single layer.

To this type belong the majority of the Dicotyledons. Helianthus annuus, Fagopyrum, Raphanus sativus, Myriophyllum, species of Salix, Casuarina stricta, Linum usitatissimum, and Primulaceæ[1] have been carefully investigated.

4. The fourth Angiospermous type (Fig. 5) is observed in those of the Cucurbitaceæ (Cucurbita) and Papilionaceæ (Pisum, Phaseolus, Cicer) which have been investigated. Here a common initial zone extends transversely over the *punctum vegetationis*; by the divisions in this arise, on the side towards the

FIG. 5.—(210) *Pisum sativum*. Median longitudinal section through the apex of the root, after Janczewski. *p*—*p* plerome, *p*—*r* periblem, *J* common transverse initial zone, *c* its lateral continuation.

root-cap, successive layers, which are added to the conical middle portion of the latter. On the side of it facing the body of the root arise a massive plerome-cylinder, and a periblem many layers of cells thick, having approximately the form of a hollow cylinder open towards the initial layer. From its margin the transverse initial zone of meristem curves itself round, so to speak, over the adjoining outer surface of the periblem, and acts here for a further space as initial layer, on the one hand

[1] Kamienski, Zur vergl. Anatomie d. Primeln, Strassburg, 1875.

for the peripheral part of the root-cap covering the sides of the apex of the root, on the other for the dermatogen-layer of the root. The origin of these, i. e. the lateral part of the root-cap, and of the dermatogen, takes place similarly to that of the corresponding parts in the third type.

II. In the Gymnosperms the differentiation of the meristem at the *punctum vegetationis* of the root[1] is essentially different from the types described for the Angiosperms (Fig. 6). A plerome-cylinder with sharp contour occupies the centre (*p–p*). The longitudinal rows of cells which compose this converge at the rounded apex towards a small initial group of cells. The plerome is surrounded by a mantle of periblem consisting of many (e. g. in Thuja occidentalis of 12–14) concentric layers arranged with considerable regularity. Each one of the inner layers (in Thuja, 8–10) of this mantle has its initial group above the apex of the plerome. The division of these cells perpendicularly to the surface (i.e. radially) brings about the increase of the surface-elements of the layer. At the same time successive divisions parallel to the surface, that is, a doubling of the layers, takes place in the apical region (Fig. 6, *i*). Since the radial walls of the successive layers fit almost exactly one on another, the cells of the periblem mantle are arranged above the apex in correspondingly regular rows. As the layers are pushed outwards above the apex by their successive doubling, division ceases in them, and increase of volume of the cells takes place; those which happen to be outermost at the apex become gradually loosened, and pushed off as a root-cap. Here then it is not possible to distinguish a layer of calyptrogen or of dermatogen; the outermost periblem acts as root-cap covering the meristematic apex. The radially arranged apical prolongation of the periblem is in all cases relatively strongly developed, its height is usually equal to or greater than the whole diameter of the root, rarely (Taxus, Cycas circinalis) it is smaller. According as it is more strongly developed, the arrangement of the cells in rows is more clearly apparent; e. g. Pinus, Ephedra, Zamia integrifolia.

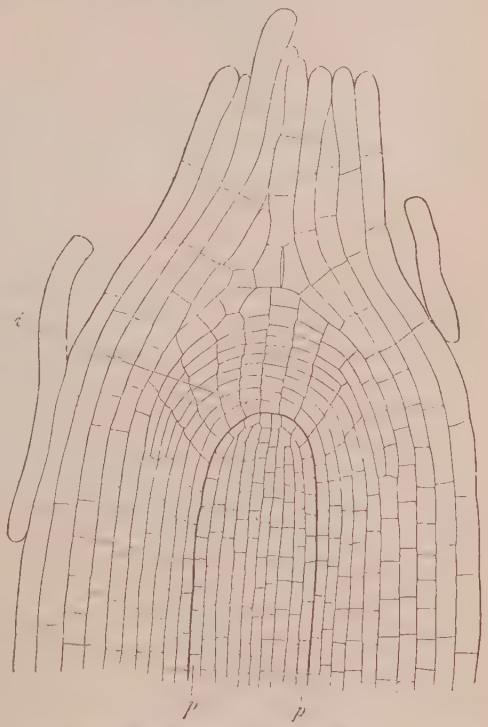

FIG. 6.—(109) *Juniperus Oxycedrus*. Median longitudinal section through the apex of a lateral root. *p–p* plerome, surrounded by about sixteen layers of periblem, the outermost of which represent the root-cap; *i* the initial region for periblem and plerome.

[1] Strasburger, Die Coniferen, &c., p. 340.—Reinke, Morpholog. Abhandl. p. 1.—Janczewski, *l.c.*

The differentiation of the meristematic apex of the stem of the Gymnosperms[1] shows a varying character, which couples it on the one hand with that which appears in the typical Angiosperms, on the other hand with that in the Lycopodiaceæ, while in Araucaria brasiliensis, also in A. Cunninghami, Dammara, and Cunninghamia, the dermatogen, periblem, and plerome remain clearly distinguished, in the extreme apex; in the Abietineæ and Cycas these layers run together into a common initial group, which occupies the extreme apex; a separation into the three layers first appears at some distance beneath this in Cycas, and more clearly in the Abietineæ. Ephedra is specially interesting, for here, in the same species (E. campylopoda) and apparently fluctuating in the same shoot, the character varies between the two extremes described. At one time there is a dermatogen-layer, sharply defined throughout its whole course, covering the two inner layers which in the extreme apex are more or less clearly separate; in other cases both merge with the dermatogen into a common superficial initial group. A series of similar cases, some corresponding to Araucaria, others approaching the other extreme, were made known by Strasburger's researches on Taxus, Podocarpus, Saxegothea, Ginkgo, Thuja, Cupressus, Sequoja, and Cryptomeria.

Here, as in the Angiosperms, the dermatogen and periblem alone take part in the origination of leaves and normal lateral shoots, and in most cases also in the same fashion as there. In the Abietineæ, however, there occur also divisions parallel to the surface in the dermatogen of the young leaf.

III. As already intimated, the differentiation of the meristematic apex of the *Lycopodiaceæ*[2] corresponds closely with that of the Gymnosperms. The extreme apex of the stem is occupied by a group consisting of 2–4 prismatic cells with their longer axis at right angles to the surface. This is the initial group for the periblem and dermatogen, or rather for a superficial layer which corresponds to the latter. All these initial cells divide by walls perpendicular to the surface, and the products of this division, as they are removed from the apex by the advance due to the growth of the latter in length, divide again parallel to the surface, forming thus the initial layers of dermatogen and periblem. A plerome-cylinder, which is limited laterally by the periblem, elongates independently through the activity of an initial group or single cell of its own, which occupies the centre of its conically tapered apex, and lies immediately beneath the initial group of the outer layers. As Hegelmaier has already asserted, conditions are to be found, which point to the origin of the initial cells of the plerome from the common initial group at the surface of the apex (by transverse division). It is thus possible that a fluctuation of the definition of layers occurs here similar to that in the Coniferæ. The formation of the leaves starts in the Lycopodiaceæ from one cell of the outermost (dermatogen) layer, which, after arching outwards, divides first parallel to the surface, then further. The differentiation of the meristematic apex of the root is, according to the investigations of Strasburger and of Bruchman, similar in the Lycopodiaceæ to that in the first type of the Angiospermous roots.

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[1] Strasburger, *l.c.* p. 323, Taf. 22, 23, 25.—Pfitzer, in Pringsheim's Jahrb. VIII. p. 56.—[Dingler, Botan. Zeitg. 1882, p. 795.]

[2] Cramer, Pflanzenphysiol. Unters. Heft III. p. 10.—Strasburger, Coniferen, p. 336.—Hegelmaier, Bot. Zeitg. 1872, p. 798 ff., 1874, p. 773.—Bruchmann, Ueber Wurzeln von Lycopodium und Isoetes, Jena, 1874.—Compare also Russow, Vergl. Unters. p. 176.

The investigations of Bruchman assign to the root of Isoetes a conformity with the third type of Angiospermous roots. According to the results of this observer, which harmonize with those of Hegelmaier [1] with the exception of one not very important difference, the apex of the stem of the Isoeteæ is occupied by a small group of initial cells, which are common to the whole meristem. Longitudinal divisions of these form the mother cells of the peripheral layers of meristem, and renew the initial cells; transverse divisions of them supply new elements to the central part of the meristem. A division into the three distinct layers cannot be seen.

Very similar to the structure of the apex of the stem of Isoetes is the differentiation of the meristem peculiar to some Selaginellas, and the roots of Marattia. It should therefore be mentioned here, but for the sake of shortness the description of it will be supplied further on [2].

IV. The stem of Isoetes and the above-named Selaginellas and Marattiaceæ form the transition between the forms of differentiation of the meristem already described, and that which prevails for the great majority of the Pteridophyta (comp. Fig. 7–9). The characteristic in these cases is this, that the entire meristem of the apex originates from one single common initial cell, which is called, from its position at the apex of stem and root, the *apical cell* [3]. Successive bipartitions divide the apical cell in each case into an apical part, which retains the original position and form, this being compensated again by growth, and remains as the apical cell; and a basal inferior part, which is added to the growing meristem. The latter part is termed the *segment-cell* [4]. Further divisions of the segment-cell form the meristem and later tissues. Each portion of meristem, which originates from a single segment-cell, is called a *segment*. In roots, besides these processes, there is in addition the formation of root-cap, which also originates from the apical cell; this must now be provisionally ignored.

The apical cell (Fig. 7–9) has in most of the present cases the form of a three-sided pyramid, with convex base, which is the apical surface (i.e. the outer wall); while the sides are sunk in the meristem. This is the case in all roots of the plants in question (except those of the Selaginellas, in which the form of the apical cell is doubtful), and in the majority of the apices of stems. In other cases the apical cell has the form of a two-edged wedge, the arched base and the point having otherwise the same arrangement relative to the other tissues as in the cases with the three-sided cell: apex of the stem of Salvinia, Azolla, many Selaginellas (S. Martensii [5], Kraussiana), and Polypodiaceæ (Pteris aquilina), Polypodium rupestre, Lingua, aureum, punctatum, phymatodes, Platycerium alcicorne, stolons of Nephrolepis undulata according to Hofmeister [6].

In the stolons of the last named species, as the apex becomes stronger, the apical cell assumes the three-sided pyramidal form. In Polypodium vulgare it alternates between the two (Hofmeister).

In the seedling of Selaginella Martensii the apical cell of the main shoot,

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[1] Bot. Zeitg. 1874, p. 481.

[2] [Holle, K. Ges. d. Wiss. zu Gött. 8 Jan. 1876.]

[3] Nägeli, Zeitschr. f. wiss. Bot. II. p. 121 (1845), III. p. 157.

[4] Pringsheim, Jahrb. f. wiss. Bot. III. p. 491.

[5] [M. Treub, Recherches sur les Organes de la Vég. du Selaginella Martensii, Leide, 1877.]

[6] Hofmeister, Beitr. zur Kenntniss der Gefässkryptogamen II. Abhandl. d. k. Sächs. Gesellsch. d. Wissensch. Bd. V.

and of the two branches of the first bifurcation, has, by reason of corresponding divisions, the form of a four-sided pyramid, which however soon passes back to the two-edged form [1].

Each segment is separated from the apical cell as a tabular cell by a division wall, which is approximately parallel to one of the sides of the apical cell. This wall is called the *principal wall* of the segment [2]. Each segment has two principal walls, one (acroscopic) by which it was separated from the apical cell, the other (basiscopic) that which adjoins an older segment. Its *outer wall* is that part of the free wall of the apical cell which is cut off by the line of junction of the acroscopic principal wall; its *lateral walls* are the parts cut off by the lines of junction of the same principal wall from the principal walls of the segments, which border it laterally.

The principal walls, which cut off the successive segments from the apical cell, are parallel *in regular succession* to the sides or principal walls of the latter. Thus in the case of a two-sided apical cell they oppose the one and the other side of it alternately, each fronting the older principal wall; in the case of a three-edged apical cell, they oppose the three sides successively in spiral sequence, each facing the third oldest principal wall, and being attached laterally to the two younger principal walls. All the segments therefore of a meristematic apex are arranged (if we ignore subsequent displacement) in as many straight rows parallel to the axis as the apical cell has sides.

The principal walls of a segment, which has recently been cut off, are inclined to the theoretically straight perpendicular axis of the meristematic apex at an acute angle, which varies according to the form of the apical cell. As growth proceeds, the form of the segment alters, and with it the direction of the principal walls (or rather the planes in which these lie), so that, with reference to a perpendicular axis, they assume a horizontal position. For a thorough discussion of these phenomena, and of the growth of the apical cell itself, cf. Nägeli and Leitgeb, *l. c.* p. 91. The figure 7 A, which is borrowed from these authors, may present the process to the eye.

The segments cut off from the apical cell become gradually divided up into masses of meristem consisting of several or many cells. As the result of the changes of form and position already mentioned as accompanying the joint growth, each of these masses represents part of a more and more horizontal disc, and meets the similarly shaped segments next in age to it at the central line. A transverse section cut at some distance from the extreme apex includes so many united segments as there are straight series of these, i.e. where the apical cell is two-sided, 2; where it is three-sided, 3. The divisions proceed rapidly, and if, as must be done in this case, one disregards lateral outgrowths, they proceed in the same direction and in the same succession in the successive segments. One thus finds the segments of each transverse section in about the same stage of division.

In those cases where the successive divisions have been successfully and accurately followed—apex of the stem of Equisetum, Azolla, Selaginella Martensii, partially also in Salvinia, and especially in the roots of Equisetum, Azolla, and many

[1] Pfeffer, Entw. d. Keims v. Selaginella.—Hanstein, Bot. Abhandl. Bd. I.

[2] Cramer, Ueber Equisetum in Nägeli und Cramer, Pflanzenphysiol. Untersuchungen, 3 Heft, p. 21 (1855).

Filices and Marsileaceæ we may distinguish in the first stages of the further development of a segment, three sorts of division, differing in their direction and results. They are:—

(1) *Divisions into flats* (Etagentheilungen), that is, splitting of the segment into similar stories one above another by division walls at least approximately parallel to the principal walls.

(2) *Radial halving*, division of a segment into halves lying side by side, but never quite alike, by an approximately (but not exactly) radial wall: in the case of segments arranged in two series, that is, which correspond in the circular transverse section to semicircles, this radial halving divides the section into (unequal) *quadrants;* in case of segments in three series, into *octants:* the walls in question are named accordingly. In the first case the division into quadrants is followed either by a second halving by octant-walls (stem of Salvinia, Azolla) or only each larger quadrant is again halved, so that each segment is divided by two radial walls into three cells (stem of Selaginella Martensii).

(3) *Division into strata* (Schichtentheilung), that is, division by tangential walls into concentric strata parallel to the surface.

These three modes of division, which appear as the first successive stages of division, are followed by further divisions in the three principal directions in each story, and in each stratum. These divisions alternating variously according to the species, finally result in the definitive composition of the segment.

Of the above three first stages of division, that marked (3) is seldom the first. Using these figures as above to express them shortly, they usually appear in the succession 1, 2, 3 (apex of the stem of Equisetum, Salvinia), or 2, 3, 1 (root of Ferns), 2, 1, 2, 3 (apex of stem of Azolla); only in the root of Azolla the succession 3, 2, &c. was found by Strasburger. Relatively to the future layers of meristem, i.e. to the later developed tissue layers, the first products of division of the segments are thus, with the exception of the last mentioned case, still common initial cells.

From the division into strata, marked (3) above, arise layers of meristem, which correspond in their arrangement to the three principal layers of the root of the Angiosperms, i. e. plerome, periblem, and dermatogen. In many cases, though not in all (e. g. in the roots of Ferns and Equisetum), these undergo a similar development to that of the similar layers of corresponding members of the Angiosperms. They are usually sharply defined, since the walls separating them (like other longitudinal walls) in the successive segments fit pretty accurately one on another. As is evident from what has been said, we have to deal, in the phenomenon in question, with more than one, at least two, successive divisions.

As is evident from the foregoing account, many differences peculiar to special cases obtain in the very first stages of division. This is the case to a still greater extent in the later stages, which bring about in the segments their definitive composition. To enter with uniform minuteness into the peculiarities of individual cases would lead us much too far. After referring to the special literature, and particularly to Strasburger's description of the many peculiarities of Azolla, we need cite here only a few examples, keeping an eye at the same time upon many relations of form, which have not been touched upon in what has gone before.

In the roots of the Equisetums, Polypodiaceæ, and Marsileaceæ (Fig. 7, 8) the division of each segment (*h*, *h*, Fig. 7) begins with the appearance of the sextant wall *s*. This stands vertically, and, as before stated, is nearly, but not exactly radial; it is attached to the middle of the outer wall of each segment, its inner edge, however, does not extend

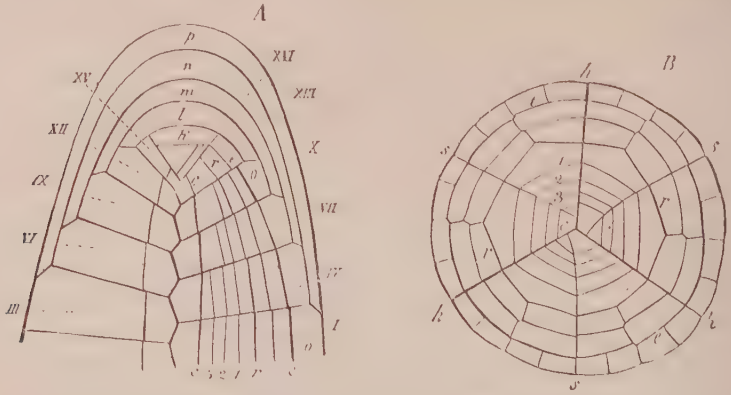

FIG. 7.—Scheme of the succession of cells in the apex of the root of Equisetum hiemale, after Nägeli and Leitgeb. *A* longitudinal section; *B* transverse section at the lower end of *A*; *h* principal walls, *s* sextant walls, *c* ('cambial wall') the first, *e* (epidermal wall) the second, *r* (cortical wall) the third tangential wall; the successive further tangential divisions between *c* and *r* are figured 1, 2, 3.

In *A* the figures I—XVI denote the successive segments; the letters *k*, *l*, *m*, *n*, *p*, the successively older portions of the root cap; *o* epidermis (dermatogen). From Sachs' Textbook.

to the central angle of the latter, but, curving slightly, meets the central part of the lateral wall further from the centre than the angle. The convexities of successive sextant walls are as a rule, but not always, homodromous, and turned toward the ascending side of the segmental spiral. The sextants of one transverse section are therefore alternately unequal in form and size, according to the distance of the point of junction of the sextant walls from the angle of the segment; among the cases observed this inequality is greatest in Equisetum, least in the Marsileaceæ. The inequality of the quadrants, octants, etc. of a transverse section from the above-named plants with two series of segments depends

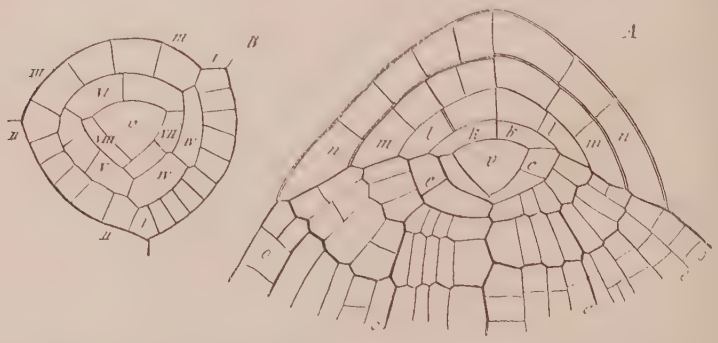

FIG. 8.—(250) A longitudinal section through the apex of the root of Pteris hastata. *B* transverse section through the apical cell of the root and the neighbouring segments of Athyrium filix femina, both after Nägeli and Leitgeb; *v* apical cell; the other letters and figures as in Fig. 7. From Sachs' Textbook.

upon similar conditions. Each sextant is in the second place divided by a tangential wall (*c*) into an inner cell which is usually small, and a larger outer one: the difference in size between the two is greater the thinner the root is, but, as stated, always so that the outer cell has the advantage. The inner cell is the initial cell of the plerome, the outer is in the

simplest cases further divided by a tangential wall (*e*) into two cells, of which the outer is the initial of the dermatogen, the other of the periblem. The dermatogen remains in the simplest cases a simple layer, since its cells suffer only radial divisions alternately horizontal and vertical, but it may also be once more divided tangentially. The two other layers are further divided and developed by successive vertical walls in definite order, which need not now be followed; later these are accompanied by transverse divisions into flats (Etagentheilung). In roots which increase much in thickness each outer cell, after the appearance of the wall *c*, may further divide by a radial vertical wall into two, in which the division by the wall *e* then takes place.

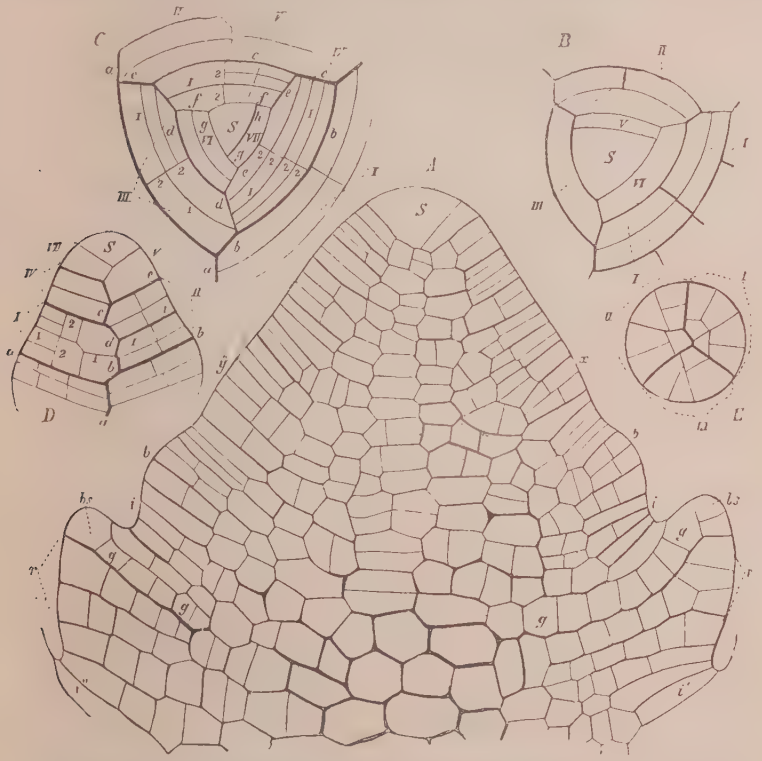

FIG. 9.—Apex of the stem of Equisetum. *A* (550) longitudinal section through a strong shoot of E. telmateja, *B* view of the apex of such a shoot from above (Sachs); *C*, *D*, *E*, from E. arvense, after Cramer; *C* a diagrammatic ground plan of the apical cell and of the youngest segment, *D* optical longitudinal section of the apex of a stem, *E* transverse section through *I* in *D*, *S* in all cases the apical cell. The Roman figures I, II, . . . (in *B* read IV for VI) indicate in all cases the segments; the Arabic figures 1, 2, 3 . . . the successive division walls within a single segment; the letters *a*, *b*, . . . in *C* and *D* the successive principal walls. In *A*, *x*, *y* indicate the highest, youngest rudiment of an annular swelling which will develope into a leaf-sheath; *b b* the same older, *b s* apical cells of a still older leaf-rudiment, *g* rows of cells from which the vascular bundles are derived, *i* the lowest layers of cells of the segments, *r* the rudiment of the cortex of the internodes; the broad central band between *g* and *g* the plerome. From Sachs' Textbook.

In the apex of the stem of species of Equisetum (Fig. 9) each segment-cell is, according to Cramer, Reess, and Sachs, divided first of all parallel to the principal walls into two nearly similar stories (*B*, *C*, *D*), then follows in each of these the division into alternately dissimilar sextants (*F*) as in the root; abnormally in many cases (comp. Reess, Pringsh. Jahrb. VI, Pl. X. 8) two sextant walls curved in different directions appear in one segment. The next division in the sextants is either a tangential perpendicular one into an outer and an inner cell, corresponding to the scheme for the root, or one not exactly radial and perpendicular, which is then followed by the tangential division (*E*). Both cases happen side

by side; the arrangement of the inner cells, which may be called initial cells of plerome, and which suffer thenceforth divisions alternately in all directions, is therefore often irregular. In the outer cells rapid divisions now follow, sometimes parallel to the principal walls, sometimes radial, and tangential-perpendicular. The definite arrangement of these is not ascertained. From these, only when they have attained a very advanced stage of development, a superficial layer is marked off, which may be called dermatogen.

In the three first stages of division of the segments (which only are well ascertained in this case), the apex of the stem of Salvinia corresponds, according to Pringsheim's statement, to that of Equisetum, with such differences as follow from the rows of segments being two in number.

For the majority of the apices of stems of the Ferns [1] it is doubtful, and requires further investigation, whether and how far the first stages of division of the segments correspond to the scheme derived from the simpler cases above described. At all events, we know from the older statements of Hofmeister (Beitr. II) that the segments undergo directly many and repeated divisions, both in directions parallel to the principal walls, and radial and tangential. By these the growing meristem is cut up into many layers and rows of cells, which are arranged similarly to the segments, but in which the boundaries of the single segments are not clear. A permanent layer of dermatogen is first distinguishable after numerous tangential divisions; a boundary between plerome and periblem is for the present doubtful.

The formation of the leaves begins, in plants which grow with an apical cell, from an initial cell cut off from a segment; and the leaf itself grows, at least in its early stages, with an apical cell which forms segments (Fig. 9 *A*, *b s*).

In the roots of the ferns in question, the formation of the cap starts also from the apical cell, and begins by the cutting off of a cell from the otherwise unaltered apical cell near its apical surface, by a wall perpendicular to the axis. This cell has the form of a flat segment of a sphere, and is the first *cap-cell* (Fig. 7, 8, *A*, *k*). This is the initial either of one of the simple layers of cells or sheaths (*l*, *m*, *n*, *p*), from a combination of which the root-cap is built up, or, by undergoing a subsequent transverse division, it is the initial of a pair of such sheaths. Each primary cap-cell is immediately divided by longitudinal walls at right angles to its outer surface, which becomes more and more convex as the growth at the apex of the root proceeds. It is divided first by a median longitudinal wall into two equal halves, these being again divided into four quadrants by a wall at right angles to the first. Each quadrant cell is again divided into two unequal parts by a longitudinal wall, which halves the outer walls, or divides them into unequal parts, and then taking a curved course inwards attaches itself to one of the lateral walls. The further divisions which appear in the eight cells of the sheath thus formed become successively more irregular, and may be followed up in the work of Nägeli and Leitgeb. Where the primary cap divides into two, this happens after the first three longitudinal divisions are completed.

According to Hofmeister, Hanstein, Nägeli, and Leitgeb, the rule is that a primary cap-cell is cut off from the apical cell after each cycle of segments, which go

[1] On the phenomena in *Ceratopteris*, which differ from those in the other Ferns in the narrower sense, compare Kny, Entwickl. d. Parkeriaceen, Abhandl. d. K. Leop. Acad. Bd. 37 (1875).

to form the body of the root. In longitudinal section therefore in the younger transverse zones, each successive segment is laterally overlapped by a new cap (or, as the case may be, by a pair of them). There are, however, exceptions to this rule. Further, each cap-cell abuts on the principal walls of the cycle of segments cut off immediately before it, and this condition remains often for a long time recognisable by this character, that each cap rests with its margin upon the step-like outer walls of two successive segments. This arrangement is obliterated sooner or later by the smoothing down of the steps resulting from growth.

We must now return to the phenomena in many Selaginellas, and in the Marattiaceæ, which were before left unexplained.

As before stated, a number of species of the first-named genus have on the stem a two-sided apical cell, which forms segments from its two sides. Russow[1] first drew attention to the fact that in many species—*e.g. S. arborescens*, *Pervillei*, *Wallichii*, *Lyallii*—there is not a single apical cell, but an apical group of common initial cells. Strasburger[2] has carefully investigated *S. Wallichii*, and found that here, in place of *one* apical cell, *two* are present, which form segments in conjunction with one another. Each of them has the form of a wedge with narrow rectangular section, and is bounded by five planes; *i.e.* two nearly equal lateral planes, in form of isosceles triangles, the bases of which are the long sides of the rectangle presented by the cell in transverse section; two narrow-rectangular lateral planes, and a fifth also narrow-rectangular, which is the free apical plane: the lateral planes, like those of simple apical cells, are sunk in the meristem. Both cells are joined by one of their broad triangular lateral faces into a double wedge of corresponding form, and the relative position of this is such that the two triangular lateral faces are perpendicular to the dorsal and ventral faces of the (bilateral) stem, while the joint wall of the pair of apical cells is in a median position. One may therefore shortly name the broad triangular faces lateral, and the narrow rectangular ones the upper and lower. Segments are formed similarly in each of the two apical cells in the following succession. First a principal wall parallel to the lateral faces cuts off a segment almost similar to the apical cell, then two narrow segments of rectangular section are cut off by principal walls parallel to the upper and lower sides. After these follow again lateral segments, &c. Thus four straight rows of segments arise, as from a single four-sided apical cell, the series right and left being wedge-shaped, while the upper and lower segments are rectangular, and are arranged in each case in a double series. The latter form the ventral and dorsal portions of the stem, the former the lateral portions.

In the Marattiaceæ the apex of the stem is as yet but little investigated. Hofmeister (Beitr. II) ascribes to *Marattia cicutæfolia* a three-sided apical cell. The meristematic apex of the root of these plants, as shown by Harting[3], and more carefully described by Russow (*l.c.*, p. 107), consists of a numerous group of large, polygonal, pyramidal, common initial cells; cap-cells are cut off from these by transverse walls near their broader, outer, or apical face: from these the root-cap is formed: near their inner face, cells are cut off which as initial cells form the plerome cylinder.

[1] Vergl. Untersuchungen, p. 176. [Cf. Schwendener, über Scheitelwachsthum mit mehreren Scheitelzellen, Botan. Zeitg. 1880, p. 716.]

[2] Botan. Zeitg. 1873, p. 115.

[3] De Vriese et Harting, Monogr. des Marattiacées, p. 41, Taf. 4.

Further they divide by longitudinal walls, which are similarly directed to their lateral faces but are otherwise apparently irregularly arranged, into daughter cells, of which those nearest the apical point always retain the properties of the common initial cells, the others, as they retreat from the apical point, form the peripheral layers of meristem, dividing first by numerous repeated tangential longitudinal walls, which are followed by others in radial and transverse directions. In this case also a separation between periblem and dermatogen appears first in an advanced stage of development.

Lastly, we may notice shortly the meristematic apex of *Psilotum*, which, according to Strasburger, shows according to the quality of the shoot, either a simple apical cell, or an initial group consisting of many members. Reference may be made to the investigations of Nägeli and Leitgeb, and of Strasburger[1].

The foregoing summary shows, first, that the similar differentiation of the meristem at the apex of stems and roots originates in a different way, that is, from different first beginnings, in the different groups of the vegetable kingdom, and in such groups as the Selaginellas and their allies, which are intermediate between the larger divisions; it originates differently even in the single species.

Returning to the question, whether in all cases only definite zones of meristem give rise to definite sorts of tissue, the most general answer, according to our present knowledge, is a distinct negative[2]. To be sure this negative does not hold for all single cases. For instance, for the large majority of roots, not only does each of the different layers of meristem correspond to a definite section of a definite system of tissue, but even the separate parts of each of these sections may often be traced back to its separate initial cells in the apical meristem. It is therefore in this case not only allowable, but preferable, for the sake of clearness, to term the layers of meristem directly the initial layers of the axile vascular strand and its parts, or of the Epidermis, &c., instead of using the terms selected above. But even in Roots exceptions occur. The Epidermis, for instance, in the Gymnosperms does not originate from a distinct dermatogen layer, so that we should properly speak of a Pseudo-epidermis, if we regard as true Epidermis only the layer of cells derived from a distinct dermatogen layer. In the aerial roots of most Orchids there arises from a distinct dermatogen layer, as will be hereafter shown, a sort of tissue different from Epidermis.

The negative, however, of the constant genesis of definite sorts of tissue, or systems of tissue, from definite zones of primary meristem, holds to a much greater extent for leaf-forming shoots. Here also it is true there are such relations. The system of vascular bundles of many stems of Phanerogams, for instance, is derived exclusively from the plerome cylinder. The plerome cylinder of the Lycopodiaceæ is transformed into the axile vascular cylinder; dermatogen means in the Phanerogams nothing further than young Epidermis, &c. But exactly the opposite also occurs. The plerome cylinder arising from the inner cells of the segments develops in *Azolla* (and *Salvinia*?) into the vascular bundle of the stem. In the stem of Equisetum[3] it develops into the—chiefly transient—axile cylinder of Parenchyma, and the system of vascular bundles develops, according to the data at hand, exclusively from the zone of periblem. And the whole of the tissues, and tissue-systems of the leaves, which

[1] Botan. Zeitg. 1873, p. 118.

[2] [Cf. Haberlandt, Entwickelungsgeschichte des mechanischen Gewebesystems d. Pflanzen, 1879.]

[3] Compare Sanio, Botan. Zeitg. 1864, p. 224.

are continuous with the similar and synonymous tissues of the plerome of the stem are formed, according to the data at hand, outside the plerome, being derived, as is the whole leaf, from the periblem and dermatogen, or from the layers of meristem corresponding in position to these. From all this we see then, that definite relations between the original differentiation of the meristem and the formation and arrangement of the definitive tissues obviously exist, but that these are not universally the same. If then the course of treatment is to be uniformly arranged, we must for the time being regard especially the *distribution* of tissues, while still keeping an eye upon the differentiation of the meristem.

In opposition to the foregoing view, another has lately been asserted, since Famintzin[1] has undertaken to prove that in the Angiosperms definite systems of tissue, namely besides the Epidermis especially the system of vascular bundles, are universally, *i. e.* in all parts of the plant, each derived from the same primary layers of meristem, which are separated even in the embryo, and develop further independently near and between one another like the germinal layers of the animal body. The layers of meristem in question are fundamentally the same above distinguished by us. On the share taken by the dermatogen in the development of tissues there can be no two opinions; the main question therefore is whether the system of vascular bundles arises universally, *i. e.* in the whole plant from the same primary layer of meristem. If we ignore isolated cases of controversy, the plerome or a certain region of it is in stem and root the initial part for the system of vascular bundles, or for the greater part of them. The question therefore is whether the parts of the system of vascular bundles, which pass from the stem-system into the leaves, and which belong to the latter, also arise from the plerome at the apex of the stem. This could not be otherwise effected than by outgrowths of the plerome pushing between the other layers of the young forming leaf, and growing with these, as was above asserted for the common growth of dermatogen and periblem. Other investigators do not find this; they rather say that the vascular bundles in the leaf, like the other inner parts of it, are derived from the primary periblem, since definite bands of the latter show the corresponding differentiation; and that they are connected with the system of the stem by reason of the relative position of the said bands of periblem[2]. Famintzin's researches certainly afford valuable conclusions on certain processes, but no new result on the main question. When he proves that in foliage leaves, especially in the Papilionaceæ, the parts of the vascular bundle always arise from quite definite layers of the meristem, he says nothing new; for as the mature vascular bundles in the leaf have a definite position, this must hold also for their younger stages. He does not produce proof that these bundle-forming layers arise as branches from the plerome layer in question of the stem, and push themselves between the other tissues of the leaf, and this proof he should have brought in order to establish his view; he communicates rather observations, which lead to the contrary result. He asserts that the leaf of the Papilionaceæ mentioned, *e. g.* species of Trifolium, at a certain age consists of five layers of meristem; the outermost is dermatogen or epidermis, of the four inner only the two innermost are points of origin of the vascular bundles. He further asserts that in an earlier stage within the dermatogen lies only *one* layer of meristem cells—which, according to our preceding statement, must be derived from the periblem of the *punctum vegetationis*; and that the four later layers arise from division of the cells of that one. It is clear that thereby the postulated pushing in is excluded, and on this the theory of germinal layers must be founded.

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[1] Botan. Zeitg. 1875, p. 501.—Beitr. zur Keimblatt-theorie im Pflanzenreich, Mem. Acad. St. Pétersbourg, 7 série, tom. XXII.—Compare also Botan. Zeitg. 1876, p. 540. [Compare further Famintzin, Embryologische Studien, Mem. Acad. St. Pétersbourg, tom. XXVI. No. 10, 1879.]

[2] Compare especially Sanio, Botan. Zeitg. 1864, *l. c.*

With the differences of differentiation of the meristem are always connected those of the mature structure: one may say obviously so, since the causes of the development of the mature structure, which are involved in the properties of the meristem, are different in every case.

But while the differences in the differentiation of the meristem correspond in each case exactly to systematic divisions, as distinguished principally on the ground of other phenomena, and especially so in the greater groups—for instance, all Ferns and Equisetums correspond just as closely, and are distinguished from other classes just as much by the differentiation of the apex of their stem and root, as by their reproductive and embryonic processes—the case is often different with the mature structure. The structure of the full-grown stem of Equisetum has no more resemblance to that of a Fern than to that of any Angiospermous plant however distantly related, as regards both external members and internal structure. Similar divergences are found on all sides between the characters of mature plants, and the embryonic or meristematic stages which indicate their relationships. Conversely, there is equally often to be found a convergence of properties of distantly connected species: and this is clearly expressed externally in the similarity of the most heterogeneous plants which live under like conditions, such as water-plants, the vegetation of steppes, and shores, &c.

The reason of these phenomena is easily understood when seen from the point of view of the theory of Descent, and has often enough been stated. The existing form of a species is determined by the inheritance of the properties of its ancestors, and by the changes which these properties undergo through the influence of the environment, *i.e.* the adaptation to the latter. The inherited properties must remain most clearly retained in those stages of ontogenetic development which through all generations are most independent of, that is most protected from external influences, and this is the case with the embryonic and meristematic stages. These recall in each species most completely and clearly the whole series of its reminiscences of descent, or, what is the same, they are more plainly different according to the divisions of the natural system than the later stages. Certainly these are also influenced by heredity, but the results of this may be obliterated and diverted from the original direction by successively accumulated adaptation.

As in the external conformation, which must at most be only incidentally touched upon here, so in the internal structure and arrangement of the tissues we may accordingly distinguish two series of phenomena. On the one hand those in which we recognise the direct effects of the environment (*phenomena of direct adaptation*), since they appear in plants of the most different affinity, as soon as they are adapted to like conditions of life; and since they may change with these conditions of life even in the same individual. It is hardly necessary to cite as proof the different forms of growth, which recur in the most unlike circles of affinity, and the anatomical peculiarities connected with these; or the remarkable similarity between species of the same habitat, which are systematically as far apart as possible: of the latter we may quote as the most prominent examples, in the first place, the water-plants, the similarities of which are independent of their systematic position, and will be often referred to in the following chapters. In the amphibious species the most remarkable varieties of general conformation appear, according as an individual, or even a part of one, lives in or out

of the water. Then we may refer to the almost identical form and structure of the roots of the large majority of plants however different systematically, and to the peculiarities, which at once appear in these, where a special adaptation takes place, as, for instance, in the aerial roots of epiphytic orchids, the prop-roots of the Pandanaceæ, Iriarteæ, &c.

On the other hand, there are often to be found phenomena in the structure as well as in the form of the vegetative organs, which may also be derived from adaptations, which have happened in some epoch or other of the phylogenetic development, but which cannot now be certainly referred to their causes; properties, which were acquired at an unknown time, and through unknown causes, are handed down to definite series of successive generations, and at the present time are characters of Species, Genera, Orders, and Classes, these corresponding to those taken from the formation of flowers, embryos, &c. Of the more obvious phenomena of this category, we may mention for example the arrangement of the vascular bundles in the stems and leaves of most of the Monocotyledons and Dicotyledons, the structure of the vascular bundles of the Ferns, of the wood in the Coniferæ, and in most Chenopodiaceæ, &c.

According to the terminology, which calls the properties, by which the divisions of the system are characterised, its characters, we may term the (unexplained) properties of this category (unexplained) *anatomical characters*.

Since the existing anatomical structure of a species is obviously the product of the combination of the two categories of properties, it is to be expected beforehand that, as with external form, in different species, it will be more identical the nearer is their affinity, and the more similar their adaptation. There are instances enough where this is the case. The Coniferæ, Filices, Chenopodiaceæ, Cucurbitaceæ may be again cited on the one hand as groups which have from every point of view a similar structure with very similar adaptation; other groups, whose genera and species have very different adaptation, show accordingly very different structural phenomena, for instance, the Ranunculaceæ (Ranunculus, Batrachium, Thalictrum, Clematis, &c.), the Primulaceæ (Lysimachia, Cyclamen, Hottonia, &c.)

To this rule however any fairly extended investigation brings to light numerous exceptions, viz. single species, genera, or groups, which, within their narrower or broader circle of allies, which follow the rule, are characterised by definite peculiarities of structure; these must, it is true, be regarded as inherited consequences of the adaptations of the special ancestors of the plants in question, which however cannot be referred to direct adaptation. Among the numerous cases, which belong to this category, and which will be mentioned in the following chapters, we may cite as examples—the structure of the stem of the Auriculas (Primula auricula, &c.), which differs so remarkably from that of the other Primulas, whose adaptations are however not very different; the wood of Strychnos, Wintera, &c. Examples of this sort show how cautious one must be in adducing and using anatomical characters for the greater systematic groups; how one must take care not to found such ideas upon the structure of a couple of casually chosen species.

The frequent occurrence of such exceptional cases makes the series of phenomena, which are to be treated comparatively, highly complicated, and makes useless the attempt, which at once suggests itself, to arrange the single sections, which treat of the forms of tissue and their distribution, rigidly either according to the different

adaptational forms, or according to the systematic divisions. Whether this attempt can ever succeed, will depend upon the results of further investigations, which shall have extended over whole families and classes, having regard more comprehensively and completely to *all* the questions concerned, than has hitherto, as a rule, been the case. According to the present state of our knowledge there remains for the statement of the anatomical peculiarities of the groups, which may be distinguished according to natural relationship or direct adaptation, only this one tolerably consistent and practicable course, to start from the tissues and their arrangement, and to introduce into the general consideration of these the rules and exceptions which obtain for the two kinds of groups above named.

PART I.

THE FORMS OF TISSUE.

CHAPTER I.

CELLULAR TISSUE.

General Introductory Remarks.

Sect. 1. The general properties of cellular tissue are indicated by this name, which has been interpreted above. A knowledge of the structure of the cell is here presupposed.

The sorts of cellular tissue are the *Epidermis* with its individual components, the *Parenchyma* with its subdivisions, and the *Cork*.

These are distinguished in the first place by their structure, further by the form, arrangement, and mutual connexion of their cells.

In earlier periods of vegetable anatomy the form both of the cells, and of the tissue elements, which are not here included under the term, was exclusively or particularly regarded, and according to it were distinguished two main categories of cellular tissue (or of tissues generally); *Parenchyma, parenchymatous tissue* with cells, that is, elements (parenchymatous cells) of nearly isodiametric form; and *Prosenchyma, Pleurenchyma* with particularly long elements, which are connected with one another laterally, and with their obliquely tapered or spindle-pointed ends (Prosenchymatous cells). Among the former were distinguished a number of subordinate forms according to the special shape, as, Merenchyma, tabular, and stellate parenchyma, &c., the detailed enumeration of which would now be purposeless [1].

One may, as is often the case, retain these names to indicate the forms; however it may be better to choose for these forms purely descriptive terms as wanted, and from this point of view to term the two above-named main categories of form on the one hand *isodiametric cells*, on the other *elongated* or *fibrous cells*.

With reference to the structure of the cells, besides the special properties, according to which the distinctions between them will hereafter be drawn, a difference

[1] Compare Meyen's Phytotomie, and Mohl, Vegetab. Zelle, p. 16.

often occurs, which concerns the relative development of mass, on the one hand of the cell walls, on the other of the protoplasmic body and the contents. On the one hand, we have cells with a relatively thin wall, and richly developed protoplasm and contents, characterised by the components of the latter—chlorophyll, starch, sugar, inulin, &c.—as the specific organs of assimilation, and of metabolism, or chiefly containing watery cell sap. On the other hand we find cells whose protoplasm and contents are reduced relatively to the strongly thickened, and often lignified membrane, and which accordingly, without giving up the properties of typical cells, or their part in the process of assimilation, obviously participate in the mechanical functions, i. e. the strengthening of the parts to which they belong. The 'Collenchyma' of the cortex of herbaceous plants and the sheaths of the vascular bundles of many monocotyledonous roots are examples of the latter condition. One can accordingly distinguish two extreme forms of structure, and call them shortly *thin-* and *thick-walled* cells, names which are explained by what has gone before. When with the thickening of the wall there appears a process of lignification—which in itself still needs to be more carefully studied—and a hardening of the wall thus occurs, this process will for the future be indicated by the term *Sclerosis*.

The different grades of wall-thickening are not generally confined to a definite cell-form, or to any one of the sorts of tissue here distinguished on completely different grounds; there exist isodiametric and fibrous cells with thin, and with sclerotic walls, sclerotic Parenchyma, Epidermis, and Cork cells, &c. But besides this, as may be concluded from what has been already stated, there is no sharp limit between the two main forms, even if one ignores the following fact, which should be brought prominently forward, that sclerosis is the commonest phenomenon of secondary metamorphosis which appears in cells.

In the large majority of cases, the species and varieties of cellular tissue are distinctly different from one another, and the treatment must start from these cases of marked differentiation and division of labour. But since all are derived from fundamentally similar meristem, and the properties of the cell remain to all alike, there appear also cases of less complete differentiation and division of labour, and transitional forms, to the existence of which attention must be directed from the very first, and which raise permanent difficulties in many single cases in the way of a sharp division of tissues.

From the non-equivalent sorts of tissue which originate by metamorphosis of cells, the cellular tissues are, irrespective of their common origin, usually quite clearly distinct. But there are two exceptions to this. Firstly, a sharp limit cannot always be drawn between *sclerotic cells* and *sclerenchyma*, which has lost the cell-quality. The secondary sclerenchyma-metamorphosis, which often appears in cells, must lead to transitional forms; and practically it is often impossible to distinguish whether the cell quality remains, or is lost. In many cases therefore the question arises whether a separation of the sclerenchyma from the cellular tissues is to be attempted at all, and to be as far as possible carried out. The frequent occurrence of sharp differentiation answers the question, I think, in the affirmative.

Secondly, intermediate cases exist between cells and the secretory reservoirs, in so far as the bodies termed secretions, which fill the latter, as oxalate of calcium, resinous bodies, &c., frequently appear also as constituents of the contents of typical

cells, and these, as the quantity of the secretion increases, become like those reservoirs. For judgment upon these intermediate forms, and the possibility of carrying out the separation of the forms of tissue, the same reflections hold good as for the sclerenchyma. The difficulties of distinguishing them in practice are, besides, much smaller in this case than in that of the sclerenchyma.

SECTION I.

EPIDERMIS.

Sect. 2. **Epidermis,** outer skin, is the name given to the layer of cells which is covered by and produces the *cuticle*. It constitutes the surface of such plants as are several layers of tissue thick, from the beginning of the differentiation of tissues onwards throughout their life, or till the beginning of the development of cork, which takes its place.

On the stems and leaves of Angiosperms the Epidermis is sharply marked off, even in the young embryo, while still consisting of few cells; in this case, as long as it remains in the meristematic condition, it is termed the Dermatogen layer. This grows, as stated on p. 7, with the stem, leaves, and branches, covering them as a cellular mantle, one layer of cells thick. It remains in the large majority of cases throughout its life a simple layer of cells, with exception of hair structures. In relatively few Angiospermous plants divisions of the young epidermal cells appear parallel to the surface, and then in a rather late stage of development; from a simple layer of cells two or several are thus formed. These assume an essentially identical structure, and are then termed *many-layered epidermis*.

Where the differentiation of the apical meristem is other than that characteristic for the stem of the Angiosperms, a permanent outer layer of meristem, derived by successive divisions from initial cells common to it and to other layers, assumes the properties of the epidermis. In plants which grow with an apical cell, definite peripheral products of division of the segments serve this purpose; in Gymnospermous roots the transverse portions of the successive layers of periblem from time to time laid bare by the separation of the root-cap, &c. Comp. above, p. 14. In these cases we cannot speak of a many-layered epidermis in the same sense as in the stem and leaf of the Angiosperms, since the genetic relations characteristic of those cases are different; that term can at most be conventionally used for single cases which in fact scarcely ever occur. In single special cases also in the Angiosperms, the epidermis originates from other elements than the dermatogen. The perforations (and indeed also the laciniæ) in the leaves of many Aroideæ originate by the early dying off of circumscribed portions of the young leaf, the original epidermis dying off with them [1]. Since the edge of the mature perforations is clothed with epidermis, this must be completed from the inner layers of the young leaf, which point moreover remains still to be more

[1] Compare Trécul, Ann. Sci. Nat. 4.sér. tom. I. p. 37.

closely investigated. Similar relations, which however also require further observation, may hold for the margins of the leaf-segments in the Palms, since these segments originate by the splitting of the continuous young lamina[1]. In one or few-layered parts, like the leaf-surfaces of the Hymenophyllaceæ[2] and Hydrilleæ[3], either there is no differentiation of the epidermis from the parenchyma, or it has been obliterated. One can in this case speak of epidermis only on the ground of the cuticular covering, which is present, or as in the two-layered leaf lamina of the Hydrilleæ, on the ground of genetic relations. In the many-layered parts also of submerged water-plants the differentiation of epidermis and parenchyma often becomes less plain, as will later be described.

In the overwhelming majority of cases the epidermis is sharply distinguished from the cells which it surrounds.

1. COMPOSITION OF THE EPIDERMIS.

Sect. 3. The following kinds of cells or cell-groups are to be distinguished as parts of the Epidermis :—

(1) *Epidermal cells.*

(2) *Stomatal, guard-cells*, pairs of which enclose a slit-shaped intercellular space, and together with this form the *stoma*.

(3) *Hair-structures* (Trichomes).

Sect. 4. **Epidermal cells** in the strict sense is the name given to those cells of the epidermis whose lateral walls are in uninterrupted connection with one another and with stomatal cells. Exceptions to this occur only in the slightly differentiated epidermis of the base of the leaf of the Osmundaceæ and Isoetes (comp. Sect. 9). The term lateral walls is here used for all those which are at right angles to the surface. With reference to the longitudinal axis of growth of the member of highest rank to which they belong, we may therefore speak of superior or inferior lateral walls, and of side or flanking walls; and, in obvious contrast to these, of outer and inner walls. The direction at right angles to the surface, i. e. that of the lateral walls, may be called the *height* of the cell; *length* and *breadth* will be used in the same sense as for the whole organ of highest rank, to which they belong.

Form of the Epidermal cells (comp. Figs. 10–20, which follow below).

a. Epidermis one layer of cells thick.

The general form of the epidermal cells is endlessly various according to the special cases. As a rule the diameters in the two directions parallel to the surface are equal, or but slightly different, in parts which grow slowly and equally in two or three dimensions, e. g. lamina of many leaves: but the longitudinal diameter is greatly developed in longitudinally extended organs, as most stems, roots, narrow linear leaves, especially of the Monocotyledons, also on the nerves

[1] Compare Mohl, Verm. Schriften, p. 177.

[2] Mettenius, Ueber d. Hymenophyllaceen, in Abhandl. d. sächs. Gesellsch. d. Wissensch. IX. p. 403.

[3] Caspary, in Pringsheim's Jahrb. I. p. 49.

and ribs of slightly elongated leaves. The opposite, that is to say, a great transverse extension, occurs but rarely in the case of the epidermal cells in longitudinally extended parts, as for instance in the leaves of Cycas, Encephalartos, Tradescantia, Crassula, Campelia, Dichorisandra[1], many Bromeliaceæ (Pholidophyllum zonatum), and as a peculiarity of stems with clearly marked nodes, as Arceuthobium, Salicornia.

The height is as a rule either much smaller than the larger, or than both of the diameters parallel to the surface, the cells are thus of the form of flat plates overlying the surface; or it is the greatest diameter of all, the cells are then prisms arranged perpendicularly to the surface; intermediate forms between these two extremes are common enough. The lateral faces are flat, and cut one another with sharp corners, so that the single cell has the form of an angular plate or prism. In other and not less common cases they are wavy and folded, in which case the hollows and protuberances of neighbouring cells fit exactly into one another[2].

The extent of the waving may vary, or undulated and flat lateral walls may both occur in equivalent parts of one and the same species, according to the adaptation to different surrounding media. Meyen[3] noticed this relation (which remains to be further followed in other connections), somewhat indefinitely it is true, for 'a large number of species of Gentiana,' in which he found the cells more wavy 'the damper the region of the atmosphere in which the plant was grown.' Conversely Askenasy[4] found in Ranunculus aquatilis and divaricatus, on the submerged form that the epidermal cells of the leaf have flat sides, on the land-form strongly undulated sides. Also on the amphibious leaves of Marsilea and Sagittaria[5] differences occur in the above-mentioned relation.

The undulation usually extends equally over the whole height of the lateral wall, but often, e. g. in leaves of grasses and Equisetum[6], only over the strip along the outer edge, while the inner part is flat. The outer and inner surfaces of the epidermal cells are flat, or to a variable extent convex; the latter either over the whole extent of the cell, or at one (e. g. leaf of Aloe margaritifolia), or two, or several (Equisetum hiemale) relatively small circumscribed spots.

Other forms than those possible within the limits laid down are more rare; e. g. spindle-shaped, elongated, on the leaves of Torreya, Ceratozamia (Kraus, *l. c.*); the often peculiarly formed *subsidiary-cells* surrounding the stomata, together with the hair structures, must be specially mentioned below.

One and the same epidermal surface often shows only epidermal cells of nearly similar form—e. g. many smooth stems. Much oftener however considerable differences occur on the same surface. (*a*) In relation to the relief of the surface, and (often connected with this) in the distribution of stomata and hairs; in angular and ribbed stems in relation to the angles, or ribs on the one hand and the faces or furrows on the other; in flat leaves and leaf-like organs in relation to the ribs

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[1] Kraus, Bau d. Cycadeenfiedern.—Pringsheim, Jahrb. II. p. 318.
[2] Treviranus, Verm. Schr. IV. p. 16.—Meyen, Phytotomie, p. 94.
[3] Phytotomie, p. 95.
[4] Botan. Zeitg. 1870, No. 13.
[5] Hildebrand, ibid. No. 1.
[6] Mohl, Verm. Schriften, p. 262.—Mettenius, Hymenophyllaceen, p. 444.

or nerves, and the spaces between these; it is a general rule, that here the epidermal cells over the stalk and ribs are longitudinally extended, and with straight sides, but between the ribs the form and direction of the predominant elongation often alter[1]; further differences occur in relation to thorns, prickles, teeth, &c. The leaves with stomata arranged together in groups (Begonia, Saxifraga sarmentosa) will be noticed below.

(*β*) Independent of relief, and of distribution of stomata and hairs. To this category belong a number of very different special cases. In the bands of epidermis free from stomata of the leaves and green stems of most Gramineæ the epidermis consists of longitudinal rows of cells, of which some are elongated; others, alternating pretty regularly with these, are short, that is, broader or at most as broad as they are long. The short ones stand singly or by twos or threes between two long ones; in the two latter cases a further inequality often occurs, in that the upper, or as the case may be the middle cell differs in form and structure from the others[2].

In the bands of epidermis, without stomata, which cover the peripheral bundles of fibres in the stem and leaves of the Cyperaceæ, Douval-Jouve found one to two longitudinal rows of epidermal cells distinguished from the rest by a less prominent outer wall, and instead an inner wall projecting inwards in form of a strongly thickened cone[3].

The cystoliths scattered in the epidermis of the Urticaceæ and Acanthaceæ (Sect. 21), the elongated sac-shaped cells rich in tannin scattered or arranged in rows between the isodiametric sinuous elements which Engler[4] found in the epidermis of Saxifraga cymbalaria and its allies and of Sedum spurium, the large solitary cells in the small-celled epidermis of the leaf of Cymodocea nodosa, and rotunda[5], are to be registered as further kindred peculiarities. Then the 'Interstitial-bands' on the under side of the lamina, between the nerves of the floating leaves of most if not all species of Marsilea, must be mentioned. They consist of at most three to five rows of epidermal cells, which are distinguished from the ordinary cells with undulating colourless walls by more elongated form, smaller size, deep golden-brown colour of the wall, and homogeneous fluid contents. Many appearances, to be described below with glands and hairs, are directly connected with these.

b. An epidermis, more than one layer of cells thick[6], appears in the simplest cases, by the division of each original epidermal cell by one or more tangential walls into chambers, which exactly fit one on another. In many cases this happens one may almost say casually to single cells, while the neighbouring cells, which resemble

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[1] Compare Kraus, *l. c.* p. 309.

[2] Compare Bot. Zeitg. 1841, p. 149, pl. I. figs. 10, 11 (Coix), 12 (Sorghum).—Pfitzer, Pringsh. Jahrb. VII. p. 555. Here the descriptions of the older writers and the discovery by Treviranus (Verm. Schr. II) and Meyen (Phytotomie, p. 312, Taf. III. 2, 3) are cited.

[3] Douval-Jouve, in Mém. de l'acad. de Montpellier, 1872, p. 227. The phenomenon appeared in all the species of the family which were investigated, i. e. of the genera *Cladium, Rhynchospora, Fuirena, Eriophorum, Schœnus, Scirpus, Galilea, Cyperus, Carex, Kyllingia, Hypolytrum, Diplasia.*

[4] Botan. Zeitg. 1871, p. 886.

[5] Magnus, ibid. 1871, p. 210.

[6] Treviranus, Verm. Schriften, IV. p. 11.—Pfitzer, in Pringsh. Jahrb. VIII. p. 16, Taf. VI.

them in other points, remain undivided, as for instance in the case represented below in Fig. 29 of Klopstockia, and that cited by Pfitzer of Tradescantia zebrina; or divided and undivided cells (i. e. one or several layered epidermis) stand side by side in about equal quantity, as on the under side of the leaf of Passerina ericoides, and the examples cited by Pfitzer of the leaf of Pittosporum Tobira, undulatum, of the stem of Elegia nuda, Ephedra altissima, monostachya. The upper surface of the leaf of Arbutus Unedo has two layers with their cells fitting one upon another (not taking into account single cells, which remain uniseriate, and undivided), those of Begonia manicata 2–3 (Pfitzer, *l. c.*), the stem of B. tomentosa 2 [1], that of Peperomia blanda 2 [2]. In the families to which the three last-named plants belong, the Piperaceæ and Begoniaceæ, and further many species of Ficus (Fig. 18), there is formed on the leaves a much stronger many-layered epidermis, which is divided and developed in a much more complicated way.

Pfitzer describes for Begonia sanguinea, ricinifolia, and peltata an epidermis of 4 to 5 layers, while that of B. Drègei and Fischeri on leaf and stem is simple, that in B. Drègei, however, consisting of very large cells. The petiole of B. manicata has a simple epidermis, with only solitary tangentially-divided cells; the lamina has on the upper surface 2–3 layers with the cells fitting one on another; the inner of these is much higher than the outer; on the under surface (Pfitzer, *l. c.* Taf. VI. 9) it has two layers, the cells of the inner being more than double as high and broad as those of the outer—this results from the fact that after the tangential division, which separates the two layers, further radial division goes on in the outer, while in the inner only growth of the cells, without division, takes place.

In the Piperaceæ the upper surface of the leaf of all Peperomias in which the point has been investigated [3] (P. pellucida, magnoliifolia, blanda, pereskiifolia, rubella, galioides, polystachya, incana, arifolia, obtusifolia, argyracea) is provided with an epidermis of more than one layer, while that of the under side is a single layer. In P. arifolia it has two, in others, *e.g.* P. blanda 2–4, in P. incana 7–8, in P. pereskiifolia 15–16 layers. The high number of layers, and, in those cases where the number is smaller, the considerable size of the cells in the inner layers, gives to the epidermis in question a vast thickness, so that it is even in P. incana thicker than the whole remaining mass of the thick fleshy leaf; in P. magnoliifolia and rubella, it exceeds several-fold the rest of the substance of the leaf, and in P. pereskiifolia it exceeds it seven-fold.

According to the species the cell-division and growth either proceed simultaneously in all the layers, so that all fit with their cells one upon another; this is the case usually in those with two layers, but also in the many-layered P. pereskiifolia, where only the outermost layer is, as the result of divisions perpendicular to the surface, smaller-celled and differently arranged from the numerous inner ones (Pfitzer *l. c.* Taf. VI. i); *or* (*e.g.* P. incana) the outer layers become smaller-celled than the inner layers, owing to numerous divisions perpendicular to the surface, and the arrangement of the cells corresponds less in the successive layers.

Of the other Piperaceæ a two-layered epidermis on the upper side of the leaf was found by Treviranus in Chavica maculata, and by Payen in Artanthe colubrina. Miq.

As in the Peperomias, so in many species of Ficus, the many-layered epidermis of both surfaces of the leaf is produced by the division of an originally single layer. This stratum becomes smaller-celled as one proceeds from the innermost to the outermost layer.

It has been described for F. bengalensis [4], elastica, ulmifolia, pectinata, ferruginea,

[1] Hildebrand, Unters. über d. Stämme d. Begoniaceen, p. 20, Taf. IV. 4.

[2] Sanio, Botan. Zeitung, 1864, p. 213.

[3] Treviranus, Verm. Schr. IV. p. 11; Physiol. I. p. 449.— Pfitzer, *l. c.* p. 26.

[4] Treviranus, Verm. Schr. IV. p. 11 (1821).

Carica, laurifolia, Neumanni, nymphæifolia, australis, lutescens, salicifolia[1]. Its thickness varies according to the species, and is on an average less on the under surface than on the upper. Certain individual cells of the original epidermis remain undivided, and grow to form the sac-shaped cystolith-cells, which project deep into the inner tissue of the leaf (§ 21). Ficus lutescens and F. ulmifolia have on the upper surface of the leaf an epidermis of two or three layers, on the under surface of only one layer (Schacht. *l. c.* p. 142, Fig. 10).

A many-layered epidermis has further been described by Nicolai[2] and Pfitzer (*l. c.*) in the roots of Crinum bracteatum and C. americanum.

Lastly, it occurs closely connected with hair structures, on many glandular spots, to be described later, *e.g.* in Passiflora, on the ends of the leaf-teeth of Drosera, etc. Comp. § 18, 20.

Sect. 5. **Stomata**[3] (comp. Fig. 10–18). Between the cells of the epidermis there lie definitely distributed pairs of cells, whose sides opposed to one another are concave, and between these a slit is left open. The slit extends through the whole height of the epidermis, forming an open communication between the surrounding medium and an intercellular space inside it, which is called the *respiratory cavity* (Athemhöhle)[4]. The apparatus consisting of the pair of cells with the slit is called a *pore* or *stoma*[5] (*Spaltöffnung*, *Porus*, *stoma*), and the cells bordering on the slit *stomatal-*, *pore-* or *guard-cells*.

The general form of the mature stoma is in surface view (with medium turgescence) usually nearly elliptical; rarely relatively narrow, usually widely-elliptical (in 162 out of 174 cases observed by Weiss); further it is in some few cases almost circular[6], the special forms being endlessly various according to the species. The irregular three- to four-cornered stomata in Salvinia and Azolla[7] form a remarkable exception to the rule: each guard-cell corresponds to one half (in case of the usual elliptical form, a longitudinal half) of the whole form; both are, under medium turgescence, curved in a half-moon or sausage-shape; they are directly connected by their ends, and by the ends and the convex sides they are joined uninterruptedly with the surrounding epidermal cells. The concave sides are turned towards one another and bound the slit, which is usually elongated in the direction of the division-wall by which the ends of the guard-cells touch one another; in Azolla on the contrary (Strasburger, *l. c.*) at right angles to this direction. The transverse section of the guard-cell (Figs. 10, 11) is generally round or forms an ellipse

[1] Meyen, Phytotomie, p. 311.—Müller's Archiv. 1839, p. 264.—Fayen, Mém. présent. à l'acad. des Sciences, tom. IX.—Schacht, Abhandl. Senckenb. Gesellsch. I.—Unger, Anatomie u. Physiol. p. 190.—Hofmeister, Pflanzenzelle, p. 180.—Weddell, Ann. des Sci. Nat. 4 sér. tom. II. p. 271.—Pfitzer, *l. c.* p. 25.

[2] Schriften der Physic. Œcon. Gesellsch. z. Königsberg, VI. p. 73.

[3] [Cf. further, L. Reinhardt, Einige Mitt. ü. d. Entw. d. Spalt., in Russian, *Ref.* Bot. Jahresber. 1879, p. 30.—Schwendener, Botan. Zeitg. 1882, p. 233.—Tschirsch, Beitr. z. vergl. Anat. d. Spalt. Apparats. Verhandl. Bot. Ver. Prov. Brandenburg, *Ref.* Bot. Centralbl. 1881. Bd. VI. p. 341. Sachs, Vorlesungen, 1882, p. 395.]

[4] Unger, Exantheme d. Pfl. p. 43.

[5] *Spaltöffnung*, Sprengel, Anleitg. z. Kenntniss. d. Gewächse; Bau und Natur d. Gewächse, p. 180. *Poren*, Hedwig, Zerstr. Abhandl. p. 116; Rudolphi, Moldenhawer. *Stomata*, De Candolle, Organograph. végétale, I. p. 78. *Stomatia*, Link, Grundlehren, p. 108. The name dermal glands (Hautdrüsen), later resumed by Link and Meyen, has hardly any further historical interest.—For the history of these parts, so often mentioned since Malpighi and Grew (Anatomy of Plants, pl. XLVIII), compare Treviranus, Physiol. I. p. 462; Meyen, Phytotomie, p. 97; Pflanzenphysiol. I. p. 271.

[6] For details compare A. Weiss, in Pringsheim's Jahrb. IV. p. 123, &c.

[7] Compare Strasburger, Pringsheim's Jahrb. V. Taf. 36: idem, Ueber Azolla, Taf. III.

variously inclined to the slit, or bluntly angular; it has usually at the united ends of the cell a different form, and also larger diameter than at the part bordering on the slit. Examples, Persoonia myrtilloides and other Proteaceæ [1], Cycas [2], Psilotum, Equisetum, Coniferæ, Restiaceæ, Grasses, Calycanthus [3], Scirpus, Iris, &c. Along the slit, but at some distance from it, run in most cases on each guard-cell two ridge-like protuberances (belonging to the membrane, see Sect. 14), one on the outer, the other on the inner surface, the corresponding ones being continuously connected at the ends of the slit. The ridges are channelled and concave on the side facing the slit, and convex on the other side, at the free edge they are sharp, and thus appear in the transverse section in the form of sharp teeth. The outer aperture, the *entrance* (Eingang), and the inner, the *exit* (Ausgang) of the slit are thus bordered by the sharp edges of the ridges; through the edge of the entrance one enters into the *front cavity* (Vorhof), which widens out between the channelled faces; through the edge of the exit into the similarly formed but usually much smaller *back cavity* (Hinterhof); the *pore-passage* (Spaltendurchgang [4]), which

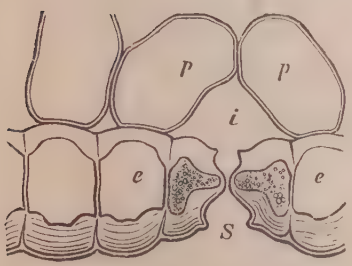

FIG. 10.—Hyacinthus orientalis, leaf, cross section. *e*—*e* epidermal cells; *s* entrance of the stoma, which has been cut through transversely in the middle; *i* respiratory cavity between the parenchymatous cells, *p*. (800). From Sachs' Textbook.

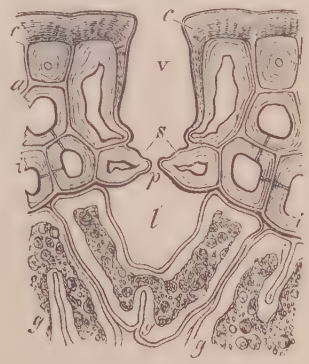

FIG. 11.—Cross section through the leaf of Pinus Pinaster. *s* guard-cells; *p* passage of the stoma; *v* the furrow, limited internally by the stoma; *c* cuticular layers; *a* limiting lamellæ between the epidermal and the hypodermal sclerenchymatous cells; *g* chlorophyll-parenchyma (800). From Sachs' Textbook.

widens towards both cavities, leads between the parts of the section of the guard-cells which are broadest, and nearest to one another, from the front to the back cavity. The ridges of exit and of entry are extremely various in form and size, (comp. Sect. 14), they are not uncommonly very small, especially the ridge of exit, and therefore easily overlooked. It is rare for both or for the ridge of exit to be really absent. The latter alone is absent in Elymus arenarius, Bromelia Caratas, Hakea saligna, ceratophylla, Banksia sp.; both in most observed Coniferæ [5] (Fig. 11), Cycadeæ [6], Ephedra, Psilotum, Azolla [7].

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[1] Mohl, Verm. Schr. p. 248. [2] Kraus, *l. c.* p. 320. [3] Pfitzer, *l. c.*

[4] 'Eigentliche Spaltöffnung,' Von Mohl, Bot. Zeitg. 1856, p. 697, Taf. XIII. Here the subject is explained. Many good drawings by Strasburger in his Beiträge z. Entwickelungsgeschichte d. Spaltöffnungen, Pringsh. Jahrb. V. p. 297, Taf. 35–42.

[5] Hildebrand, Bot. Zeitg. 1860, Taf. IV.—Strasburger, *loc. cit.* fig. 145.

[6] Kraus, *l. c.*—Strasburger, fig. 143. [7] Strasburger, Ueber Azolla, Taf. III.

The size of the mature, full-grown stomata is usually smaller than the average size of the adjoining epidermal cells, often extremely small in comparison with these, e.g. Salvinia; on the same surface, e.g. the leaf-surface, it is in the majority of cases on the whole uniform with slight variations. The absolute size of the space which they occupy in the epidermal surface lies, according to the measurements made by A. Weiss[1] on 150 plants, between 0·00011 mm □ (Amarantus caudatus; length and breadth =0·016 mm) and 0·00459 mm □ (Amaryllis formosissima, length 0·074, breadth 0·079 mm), in most cases between 0.0002 mm □ and 0·0008 mm □. The size of the open slit apparently bears an almost constant relation to that of the whole apparatus, but exact measurements of this have been made only for few cases.

The size and form of the slit as well as of the guard-cells vary regularly in the same stoma, according to the turgescence and tension of the membranes of the guard-cells themselves and of the surrounding epidermis; this turgescence and tension depending upon the supply of water, and the effect of light and heat. The curvature of the side of the guard-cells next the slit, and accordingly the opening of the slit, may in each special case increase to a definite maximum, and on the other hand diminish till the slit is completely and firmly closed. With these changes of curvature changes in the general form of the guard-cells are in each case connected. According to H. v. Mohl insolation and supply of water, according to N. Müller heat and supply of water, bring about the widening of the slit[2]. The very large stomata of Lilium martagon, candidum and bulbiferum, widen the slit, according to Mohl, to a breadth of $^1/_{170}$ mm to $^1/_{124}$ mm on the uninjured leaf, at the margins of separated pieces of epidermis to $^1/_{38}$ mm; on the uninjured leaf of Zea mais to $^1/_{178}$ mm; on the separated epidermis of Amaryllis formosissima to $^1/_{58}$ mm. The slit remains meanwhile always at least six to seven times longer than broad. Unger[3] quotes the size of the open slit in Agapanthus umbellatus at 0·000047 mm □, of Ajuga genevensis at 0.0000137 mm □.

The water-pores to be described below (Sect. 8) assume much larger dimensions, as also the stomata on the leaf of the Kaulfussias. The latter are visible to the naked eye as round holes, which are surrounded moreover by a pair of guard-cells apparently incapable of change of curvature.

The absolute height of the guard-cells, after what has been already said, requires no description. Compared with the epidermal cells, or the many-layered epidermis of the same surface, the height of the guard-cells is usually insignificant, often very small; at most they are of equal height with them (e.g. Hyacinthus orientalis[4]), Lilium candidum[5], Helleborus niger, Fuchsia[6] (Fig. 10). The position of stomata relatively to the outer surface of the epidermis is closely connected with these differences. When the height of the guard-cells is equal to that of the epidermal cells the outer surfaces of both lie approximately in the same plane. The same occurs in a series of cases where the height is unequal; here the respiratory

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[1] Pringsheim's Jahrb. IV.

[2] Compare on the mechanism, which must not here be discussed, and which is not even yet fully explained, the fundamental work of Mohl, Botan. Zeitg. 1856, p. 697; Sachs, vol. IV of this Handbook, p. 255; N. Müller, in Pringsh Jahrb. VIII. p. 75. [Schwendener, *l. c.*]

[3] Anat. und Physiol. p. 334.

[4] Strasburger, *l. c.* fig. 14.

[5] Mohl, *l. c.* fig. 6.

[6] Unger, Anat. und Physiol. p. 190.

cavity situated beneath the stoma is directly bounded by the lateral walls of the neighbouring epidermal cells, e.g. the leaves of Orchis latifolia (Von Mohl, *l. c.*), the very large-celled epidermis of the leaf of the Commelinaceæ (Strasburger, *l. c.* Fig. 150), Claytonia perfoliata (l. c. Fig. 120), and many others.

More commonly where the height is unequal, the guard-cells lie so that their inner walls fall approximately in the same plane as those of the epidermal cells (comp. Figs. 11, 18, &c.). They form then the bottom of a depression, through which one approaches the stoma from without. This is surrounded by the neighbouring epidermal cells, and is often over-arched at its outer margin by outgrowths of these, so that the mouth is considerably reduced. This is the case in the majority of tough-skinned leaves and green stems; leaf of Polypodium lingua [1], Equiseta cryptopora (comp. our Fig. 23, Sanio, Linnæa 29, 385, Taf. III. Milde, Monographia Equisetor.), Coniferæ [2], Cycadeæ (Kraus. *l. c.*), Monocotyledons, as Aloe [3], Agave [4], Dasylirion, Hechtia [5], Iris [6], Allium, Orchidaceæ, &c., and Dicotyledons, as

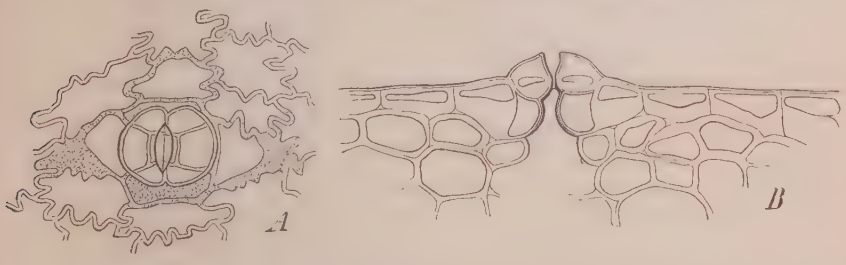

FIG. 12.—Pholidophyllum zonatum, adult leaf, under surface. *A* superficial view of a piece of Epidermis with a stoma and its subsidiary cells. *B* median transverse section through a stoma; the guard-cells are pushed outwards by the lateral subsidiary cells, which have been pushed down beneath them (390).

Ficus elastica [7], australis, Proteaceæ [8], Nelumbium [9], Dianthus Caryophyllus, and many others.

Independently of this relation of height the case occurs that the surrounding epidermal cells are so pressed against the stoma that the latter rises a greater or less distance into the air above the outer surface of the epidermis, e. g. leaves of Chrysodium vulgare [10], Aneimia Phyllitidis, hirta [11], Pholidophyllum zonatum (Figs. 12–16), Nerium Oleander, many Proteaceæ [12], Helleborus fœtidus [13], Rhinanthus, species of Primula, many Labiatæ, Pyrethrum inodorum, &c.

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[1] Rauter, Entw. d. Spaltöffn. von Aneimia, u. Niphobolus. Mittheil. d. natur. Vereins f. Steiermark. Bd. II. Heft 2 (1870).

[2] Hildebrand, Bot. Zeit. 1860, Taf. IV.

[3] Schacht. Lehrb. Taf. III. p. 24.—Strasburger, *l. c.* figs. 114, 115.

[4] Moldenhawer, Beitr. p. 103.—Oudemans, Comptes rendus, Acad. roy. Amsterdam, vol. XIV (1862).

[5] Schacht. *l. c.* Taf. IV. pp. 9, 12.—Unger, Anat. u. Phys. p. 192.

[6] Unger, *l. c.* p. 191.—Mohl, Verm. Schr. Taf. VIII.

[7] Strasburger, *l. c.* fig. 133.

[8] Von Mohl, Ueber d. Spaltöff. d. Proteaceen, N. Act, Acad. Leopold. XVI. II, and Verm. Schrift. p. 245, Taf. VII. VIII.

[9] Schleiden, Grundzüge, 3 Aufl. 1. p. 278.

[10] Strasburger, *l. c.* figs. 47, 48.

[11] *l. c.* figs. 50, 57.

[12] Von Mohl, Spaltöffn. d. Proteaceen, *l. c.*

[13] Von Mohl, *l. c.* figs. 20, 21.

From these examples, which might easily be multiplied, the conclusion is drawn that the superficial position of the stomata is the rule for herbaceous less thick-skinned parts, and the depressed position for leathery, succulent, and thick-skinned parts; but that this is by no means the case without exception. Further, that corresponding parts of plants of the same family, otherwise of like nature, such as the firm leaves of the Proteaceæ and Bromeliaceæ, may show the most extreme diversity. As an instructive example the tender-skinned leaves of Salvinia natans may here be cited, the small stomata of which are inserted about half way up the epidermal cells, which are eight to nine times their height[1].

It is obvious that when the lateral wall of an epidermal cell abuts on a guard-cell, it must present a difference of form and direction, which is in many cases very slight, from those lateral walls which do not border on stomata. The relations of height of the abutting face follow from what has been said above. The abutting face is in the one series of cases nearly plane, and set perpendicular to the surface, or inclined obliquely to it, in such a way that it converges with the corresponding face on the other side of the stoma, towards the inner face. Both arrangements occur in stomata which are even with the surface, the latter especially in stomata which project outwards. Still cases occur of stomata seated in deep hollows, which abut on their subsidiary cells with a plane perpendicular face[2]. In other cases the abutting face is concave towards the stoma, and the guard-cells are fitted into the hollow with their convex side, and are therefore more or less completely enclosed by their neighbours. With this is always connected a depression of the stoma (often only slight) below the outer surface: Iris, Amaryllis formosissima[3], Gramineæ, &c. In deeply depressed stomata (cf. the examples given above), also in Iris and similar cases, it often happens that the abutting faces are inclined obliquely towards the outer surface, so that they diverge inwards on both sides of the stomata. In this case it comes about that the guard-cells lie mainly on the inner side of the neighbouring cells (compare below, Fig. 24, Equisetum).

Irrespective of the faces just described abutting on the stoma, the neighbouring cells are in many cases of fundamentally similar form to those epidermal cells of the same surface which do not abut on stomata, e.g. Lilium, Orchis[4], Hyacinthus, Helleborus, Pœonia, Vicia Faba, Sambucus nigra, many Ferns, Salvinia, and many other plants from the most different families[5]. But in a large number of epidermal layers, especially of foliage leaves, each stoma is on the other hand bounded by one or two or several epidermal cells, differing in form and size from the rest which do not abut on stomata: these not unfrequently resemble the guard-cells themselves. These peculiar neighbouring cells of the stomata are termed its *subsidiary cells*, or *subsidiary cells of the pore*[6].

Their superficial form is generally intermediate between that of the guard-cells and the epidermal cells, or they completely resemble the first. In the latter case the

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[1] Strasburger, *l. c.* Taf. XXXVI. figs. 29, 30.

[2] Restio diffusus, fasciculatus, Pfitzer in Pringsheim's Jahrb. VII, Taf. XXVII. figs. 1–5.

[3] Von Mohl, Botan. Zeitg. 1856, Taf. XIII. figs. 2, 4.

[4] Von Mohl, Botan. Zeitg. 1856.

[5] Compare Strasburger, *l. c.*

[6] *Cellulæ laterales.* H. Krocker, de pl. epidermide. Pfitzer, Pringsheim's Jahrb. VII. p. 536.—Compare also Botan. Zeitg. 1871, p. 133; Hülfsporenzellen, Strasburger, *l. c.*

arrangement is such that the whole convex side of each guard-cell is bordered by one subsidiary cell; the stoma thus appears to be surrounded by two pairs of cells, one pair bounding the slit, and one peripheral to these (e.g. Gramineæ, Proteaceæ, and the other examples of two lateral subsidiary cells to be cited below); often even by three pairs, since the first pair of subsidiary cells is often surrounded by a second similar pair (Hakea ceratophylla, saligna [1], &c.).

If there be a difference of height between the guard-cells and the epidermis, the subsidiary cells often hold an intermediate position also in this respect; where the difference in height is great, they are of equal height to the guard-cells, or a little higher, and with them are fitted either in the outer surface, or at the bottom of the depression. Rarely the subsidiary cells are much higher than the epidermal cells; this is the case in the Scitamineæ (Strelitzia ovata, Heliconia farinosa, cf. Bot. Ztg. 1871, Taf. I. and our Fig. 28 B), where they connect the stoma with the Epidermis and Hypoderma.

The arrangement of the subsidiary cells may be most intelligibly described in connection with the history of their development, and that of the stoma; this shall therefore here be given.

The stoma itself makes its appearance by the bisection of a cell of the epidermis, which may be called its *Mother-cell* [2]. The two products of division are the guard-cells. When they separate from one another, as will be described below, a chink appears between them.

The development of the stomata takes place in the epidermis at the close of its meristematic (dermatogen-) stage and not quite simultaneously in neighbouring parts, so that one may find the most different stages of development close side by side.

The origination of the stomata begins thus: The hitherto almost similar polyhedral cells of the meristematic dermatogen are arranged in longitudinal rows, or irregularly: either all, or the majority or only single ones of these divide into two dissimilar daughter-cells. One of these becomes the *Initial cell* of the stoma, the other an Epidermal cell. Where the dermatogen-cells form rows, it is as a rule [3] always the apical, or peripheral part of the cell, which becomes the Initial cell. Exceptions to this are only known among those abnormalities or deformities which will be described below as twin stomata. Where the serial arrangement of the dermatogen-cells is absent, the relative position of the initial cells is also indefinite.

The wall which cuts off the initial cell is perpendicular to the Epidermis, or originally only slightly oblique; it either stretches as a plane (transverse-) wall between two lateral walls of the developing dermatogen-cells; or it is curved in surface view to a U-form, and then with its two ends it is attached either to one or two lateral faces of neighbouring epidermal cells, or (as a rule in Aneimia) it has the form of a closed ring, which touches no lateral wall. In the last case the initial cell is surrounded laterally by a ring-shaped cell, in the preceding case by a cell of more or less horseshoe shape.

In the further growth the three following chief cases occur:—

1. The Initial cell is the direct Mother-cell of the stoma, and the epidermal cells undergo no further division. This is the case in Iris, Hyacinthus, Orchis, Sambucus nigra, Ruta graveolens, Salvinia natans, Selaginella denticulata, Asplenium furcatum; Silene inflata, Chrysodium vulgare, the two last have a U-formed wall, the others a plane division-wall [4]: further Aneimia has as a rule an annular wall.

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[1] Von Mohl, Spaltöffn. d. Proteaceen, *l. c.*; Strasburger, *l. c.*

[2] Specialmutterzelle, Strasburger, *l. c.*

[3] Strasburger, *l. c.*; Pfitzer, *l. c.*

[4] Compare Strasburger, *l. c.*

2. The Initial cell is the direct Mother-cell of the stoma. Soon after it is marked off, along each of its sides a narrow piece of the neighbouring epidermal cells is cut off by walls running nearly parallel to each of the sides: and this takes place—

a. Once in each of the contiguous cells: of these there are four, two bordering on the ends, and one on each of the flanks of the stoma: there are therefore four subsidiary cells corresponding in arrangement to these: Tradescantia[1], species of Commelyna (Fig. 13), Pothos crassinervia (usually), Pholidophyllum (see Fig. 12), Heliconia farinosa[2], Araucaria imbricata[3]; or 4, 5, and more: Ficus elastica (4–5), Coniferæ[3], Cycas, etc.; also Strelitzia ovata (Fig. 28 A).

b. Once in each cell bordering the flanks, so that the stoma is enclosed on either side by a subsidiary cell similar to the guard-cells. This is the case in Gramineæ (probably

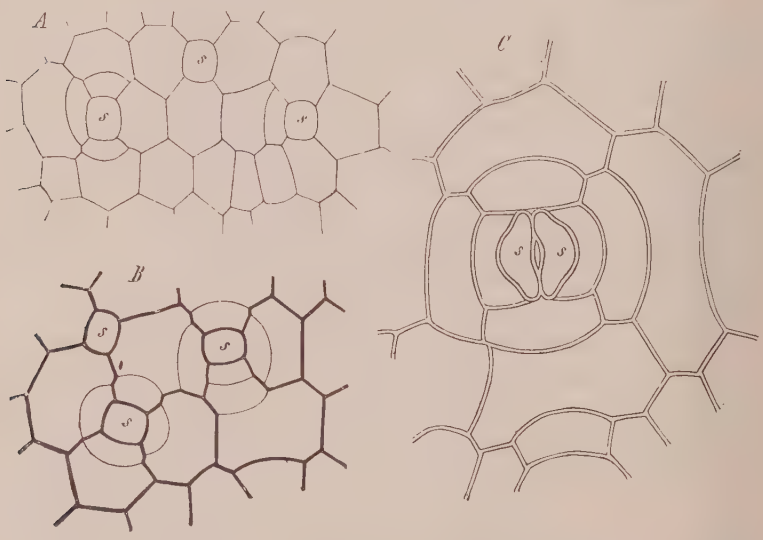

FIG. 13.—Commelyna cœlestis; leaf, development of the stomata and subsidiary cells, surface view *A* very young, *B* older stage; *s* in both the initial- and at the same time mother-cell of the stoma; *C* mature, *S* guard-cells. From Sachs' Textbook.

all[4]) and the foliage parts of other grass-like plants (Carex, Cyperus, Scirpus, Juncus lamprocarpus, effusus, Luzula maxima), Stanhopea, Aloe soccotrina, nigricans, Musa sapientum[5], Claytonia perfoliata, Proteaceæ (Protea[6]), Grevillea robusta[5], Lomatia longifolia, etc.

c. By repeated division of the subsidiary cells separated as in *a* and *b*, there arises in many cases a double zone or a pair of subsidiary cells on each side. The former is the case in Dioon[7], the latter in Maranta bicolor, Commelyna communis, Pothos argyræa, Hakea saligna, ceratophylla, and other Proteaceæ (Strasburger *l. c.*).

3. The Initial cell is not the Mother-cell of the stoma, but divides further, once or several times in succession, and the result of these divisions is a Mother-cell of the stoma, and one or several subsidiary cells. The chief types of this are:—

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[1] Strasburger, *l. c.*—Moldenhawer, Beitr. Tab. V. p. 94.—Meyen, Physiol. Tab. V; Phytotomie, Tab. III. pp. 4, 5.—Schleiden, Grundz. 3 Aufl. I. p. 277.

[2] Botan. Zeitg. 1871, Taf. I.

[3] Strasburger, *l. c.*—Hildebrand, Botan. Zeitg. 1860, Taf. II.

[4] Pfitzer, in Pringsheim's Jahrb. VII. p. 533, &c.

[5] Strasburger, *l. c.* [6] Mohl, Spaltöffn. d. Proteaceen, *l. c.* [7] Kraus, *l. c.* p. 335.

a. The Initial cell, bounded by a curved, or even U-shaped wall, is again divided by a wall almost similar to the latter into a Mother-cell and a horseshoe-shaped subsidiary cell (Asplenium bulbiferum [1], Pteris flabellata (Fig. 14), cretica [2]); or successively by 2–3 curved walls, which alternate in two directions in the surface, and cut one another, into a mother-cell, surrounded by a zone (or in parts a double zone) of half ring- or horseshoe-shaped subsidiary cells. The longitudinal axis of the subsequent slit is parallel to the chords of the previous curves of division: Cibotium Scheidei (Hildebrand, *l. c.* Fig. 37–39), Mercurialis perennis, ambigua, Pharbitis hispida, Basella, Pereskia aculenta; or

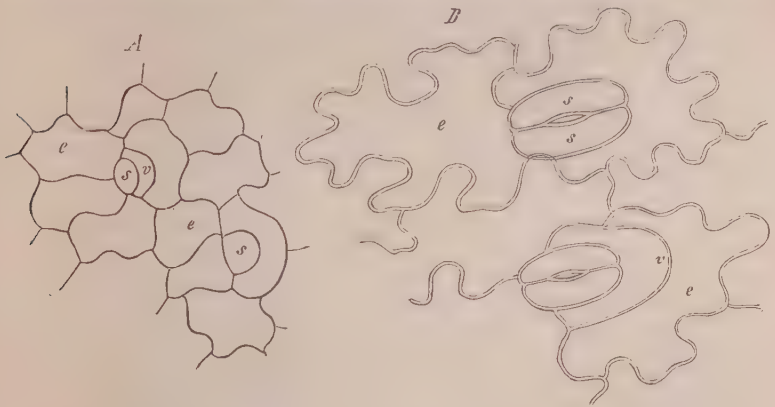

FIG. 14.—Leaf of Pteris flabellata, surface view. *A* very young, *e* epidermal cells; *v* subsidiary cell, *s* (close to *v*) mother-cell, the other *s* initial cell of the stoma. *B* almost mature, *s* guard-cells, *v* and *e* as in *A*. From Sachs' Textbook.

it cuts them at right angles: Thymus serpyllum, Physostegia virginiana, and other Labiatæ (Strasburger, *l. c.*). In the last category but one are also the Equiseta.

b. The Initial cell is divided successively by walls arranged in three directions in the surface into a simple or multiple zone of subsidiary cells, and a mother-cell surrounded

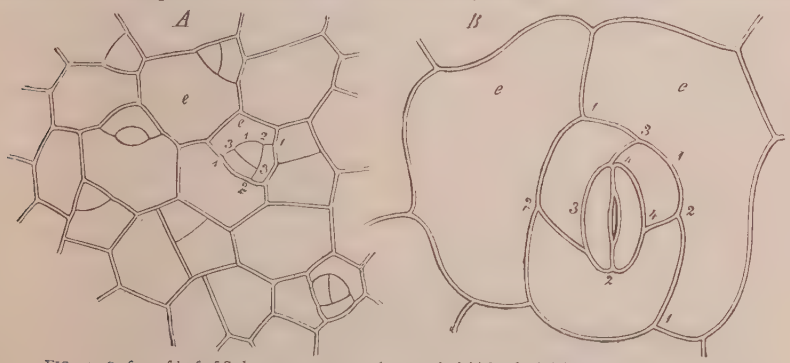

FIG. 15.—Surface of leaf of Sedum purpurasceus. *A* young, the initial and subsidiary cells arising by division of the epidermal cells (*e*); in three of the latter the initial cell is just marked off, in four others these are further divided; the numbers indicate the successive division walls. *B* almost mature, *e* and numbers as in *A*. From Sachs' Textbook.

by it. With few subsidiary cells: Papilionaceæ, Solanaceæ, Asperifoliæ, Cruciferæ; with a large number of them: Crassulaceæ (Fig. 15), Begoniaceæ [3], also Cactaceæ.

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[1] Strasburger, *l. c.* figs. 36–41.

[2] Hildebrand, Botan. Zeitg. 1866, Taf. X, fig. 20–23.

[3] Strasburger, *l. c.*—Compare for details this work so often cited; also the not always precise statements of Karelstschikoff, Zur Entw. der Spaltöffnungen, Bull. Soc. Imp. de Moscou, 1866.

c. Initial cell divided by an annular wall into Mother-cell and annular subsidiary cell: Polypodium lingua (Rauter, *l. c.*).

According to what has been said, subsidiary cells of special form originate in all the cases given under 2 and 3: in those under 1 only when the U- or annular-form of the first boundary wall necessitates special peculiarities of form. The mode of formation may be always recognised in the known cases in the mature state, but with varying sharpness, according as the subsequent growth of the cells in surface and height sharpens, retains, or obliterates the original distinctions.

Oscillations and transitions between the related types are by no means rare. For details comp. Strasburger and Pfitzer *l. c.* As regards occasional malformations, we must here again return to the twin stomata, *i. e.* those which appear in contiguous pairs, and refer to Pfitzer's detailed statement [1], according to which these may arise by means of many different anomalies of division.

Two normal exceptions must here be somewhat more carefully described. First that of Aneimia, discovered by Link, later for a long time much discussed, and misunderstood, and finally explained by Rauter, who showed that the same was the case in

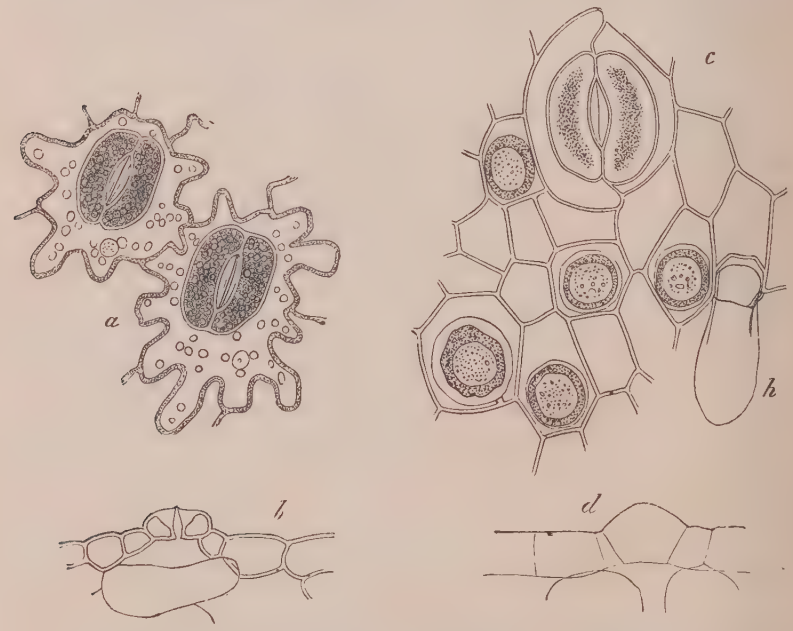

FIG. 16.—Aneimia hirta; leaf, epidermis. *a*, *b* mature; *a* surface view, *b* section perpendicular to the surface, median through the stoma (375). *c*, *d* very young (600); *c* surface view with one fully-developed stoma, and five mother-cells as yet undivided; the protoplasm of these has contracted from the delicate membrane through the process of preparation; *h* unicellular hair; *d* perpendicular section through a mother-cell of a stoma with the surrounding cells.

Polypodium lingua. In these cases the stoma is surrounded by *one* annular Epidermal- or subsidiary cell [2].

The remarkable point in this phenomenon is nothing more than that the wall of the mother-cell in normal cases has the form of a ring set at right angles to the surface,

[1] Pringsheim's Jahrb. VII. p. 551.

[2] Link, Ausgewählte anatom. Abbildungen, Heft III. Taf. IV. 8.—Oudemans, Bulletin du Congrès de Botanique, &c. à Amsterdam, 1865, p. 85.—Hildebrand, Botan. Zeitg. 1866, p. 245.—Strasburger, in Pringsheim's Jahrb. V. *l. c.*; also VII. p. 393, Anm.—Rauter, *l. c.*

between the outer and inner wall, which touches no lateral wall, and which diminishes conically inwards. In Aneimia (Fig. 16) it, or rather the stoma, is therefore surrounded by an annular epidermal cell. Almost the same applies for Polypodium lingua (see above, 3. *c*); the annular cell is in its turn as a rule surrounded by a horse-shoe-shaped neighbour, from which it was originally separated by a U-shaped wall. But often (Rauter, Fig. 18) also this wall is not U-shaped, but annular, the stoma is thus surrounded by two concentric annular cells. In Aneimia Phyllitidis, and hirta, as in Polypodium lingua, it happens exceptionally, and in Aneimia villosa (according to Strasburger) it is the rule that the typically annular walls are U-shaped, and attached to a lateral wall. Those of the mature parts are arranged accordingly. Further it occurs not unfrequently that from one or from both ends of the stoma (and in the former case, according to Strasburger, always the peripheral end) a membrane runs bridge-wise to the nearest lateral wall (Fig. 16, *c*). In face of the many attempts to explain and interpret this phenomenon it may be remarked, that from the first there is nothing more than the appearance shows at once, that is a membranous band, arranged as described, growing with the other membranes, and requiring an explanation of its appearance no more and no less than any other membrane.

The second case, which is to a certain extent peculiar, but which otherwise belongs to the group (3. *a*), is the formation of the stoma of the Equiseta. It is here stated according to Strasburger (*l.c.*). The Initial cell, the first appearance of which was not observed, is nearly cubical, the two flanks being parallel to the longitudinal axis of the stem. Near to its own longitudinal axis, thus defined, there appear symmetrically, right and left, two nearly radial longitudinal walls: both are concave on the sides facing one another, and contiguous at their upper and lower ends. The initial cell is thus divided

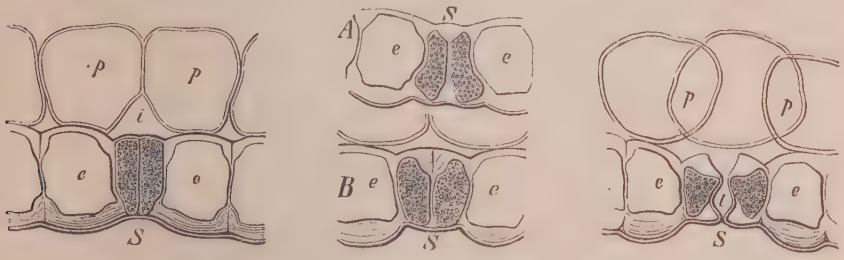

FIG. 17.—Development of the stoma of Hyacinthus orientalis. On the left the mother-cell, just divided; *A*, *B* successive further stages of development; on the right the formation of the slit is complete (*t*); the other letters as in Fig. 10, which should be compared (800). From Sachs' Textbook.

into one central biconvex-, and two lateral plano-convex daughter-cells; the two latter lessening wedge-wise inwards, the central one outwards. The central cell is the mother cell of the stoma (it divides later by a longitudinal wall into the two guard-cells), the two lateral ones are the subsidiary cells. The latter assume a form exactly similar to the guard-cells, and over-arch them, so that they cover their whole outer surface, and only leave a narrow space free above the true entrance of the stoma. Hence the form of the double pair of guard-cells apparently covering one another. In the Equiseta cryptopora of Milde the matter is further complicated by the depression of the stoma with its subsidiary cells (comp. below, Fig. 23).

To form the stoma, the mother-cell divides—after, rarely before the completion of the last division, which produces subsidiary cells—into two halves, which are the guard-cells; and the slit appears thus: the division wall between the two splits in its central part into two lamellæ which gradually separate from one another (Fig. 17). This separation proceeds from the middle towards the ends, and from the entrance and exit

towards the passage of the future slit[1]. The free edges of the ridges of exit and entrance correspond to the inner and outer edge of the original wall of division. The origin of the respiratory cavity by separation of the sub-epidermal cells precedes the formation of the slit.

The mother-cell of the stoma and the products of its division are of equal height with the other epidermal cells, and lie in the same plane as they. The subsequent various unevenness of height and position of epidermal- and subsidiary-cells and of stomata arises through the growth of the cells subsequently to their division. During growth all cells without exception increase in volume. But the passive tension by the internal tissue, which the epidermis of growing, as also of adult parts undergoes, finally brings about, as Pfitzer has shown in the stomata of the Grasses[2], a considerable

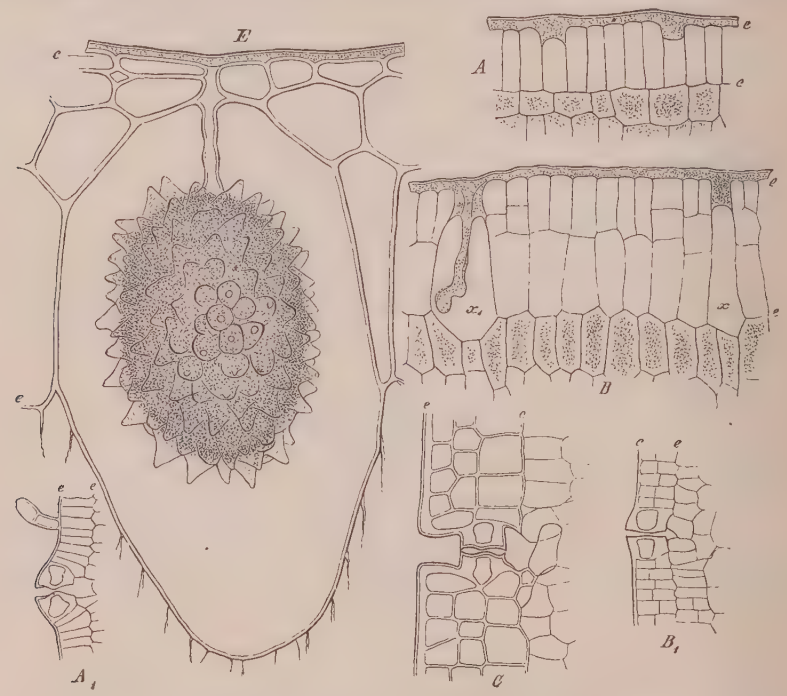

FIG. 18.—Ficus elastica; leaf, transverse section. *e—e* in each case the thickness of the epidermis; *A* (600) upper side, A_1 (390) under side of the same very young leaf; in A_1 a mature stoma, which remains superficial, and a (transitory) hair; in *A* two cystolith-cells, recognisable by their thickened outer wall, epidermal cells still undivided. *B* (600) upper side, B_1 (390) under side of a somewhat older leaf, epidermal cells dividing. In *B*, *x* is a younger cystolith-cell, and x_1 an older one which shows the peg-shaped outgrowth of the wall. *C* (390) older leaf, under side; division of now three-layered epidermis is ended, stoma depressed, but the final size and form of the parts is not yet attained. *E* upper side of a mature leaf, four-layered epidermis, cystolith-cell (375).

diminution of the absolute height and breadth of the part of the stomatal cells which border the slit. (In Zea Mais the breadth soon after the appearance of the slit amounts to 11·4 μ, later to 11·6 μ, in the mature state to 5·4 μ.) The same will apply for the other cases above alluded to, in which the part of the guard-cells bordering the slit is narrower and smaller than the connected ends.

All the phenomena of development here touched upon are the same, whether the epidermis consists of a single layer, or of several. Only in the latter case (Fig. 18)

[1] Von Mohl, Verm. Schriften, pp. 254–257.—Strasburger, *l. c.* p. 308.—Pfitzer, Pringsheim's Jahrb. VII. *l. c.*

[2] Pringsheim's Jahrb. VII. *l. c.*

tangential divisions accompany the extension of the epidermal cells perpendicularly to the surface, either successively from within outwards (Ficus), or the converse (Begonia, Peperomia). The extension and division of the epidermal cells above mentioned always begins after the differentiation of the initial cells of the stomata. The stoma itself remains, so to speak, always a single layer, the same is the case with the cells immediately surrounding it (subsidiary cells) in Begonia[1], but in Ficus, tangential divisions appear also in the subsidiary cells, which arise according to the type (2, *a*); hence a ring of subsidiary cells two or three layers deep[2]. In the growth of the epidermis perpendicular to the surface this difference here occurs, that single stomata fully developed at first, before the tangential division begins, remain at the surface; the majority are matured later, and are deeply depressed below it (comp. Fig. 18). The superficial stomata first developed are surrounded by several partitioned zones of subsidiary cells.

For the relative position of the stomata the rule holds, that in elongated parts all the slits run parallel to the longitudinal axis. In parts which do not grow specially in length the slits are arranged apparently without rule in different directions. Exceptions to this rule are the stomata on the stems of Viscum album[3], Cassytha, Thesium, Choretrum, Mida, Myoschilus, Anthobolus, Exocarpus, Arceuthobium, Antidaphne, Loranthus, Lepidoceras, Nuytsia[4], Colletia[5], Santalum album, Salicornia[6], Casuarina[7], Staphylea pinnata, on the under side of the leaf of Philesia buxifolia. Here the slits run perpendicular to the axis of the whole organ, often (e.g. Salicornia, Arceuthobium, Colletia, Philesia) the epidermal cells are at the same time extended transversely.

Sect. 6. According to special differences of form, structure, and arrangement, two varieties of stoma may be distinguished, which may briefly be termed *air-pores* (or stomata), and *water-pores*. Both may occur separately, or side by side in one piece of Epidermis.

Sect. 7. The **air-pores** show the slit itself, during normal vegetation, filled with air; they lead from the surrounding medium directly into the respiratory cavity, which is also filled with air. Its guard-cells are, with exception of the abnormal case of Kaulfussia, we may say always capable of change of curvature, and the slit therefore of variable dilatation. They represent accordingly to a certain extent openings in the epidermis which are capable of closing, through which the air enclosed in the plant communicates with that surrounding it. Their arrangement, presence, and absence are thereby generally defined.

Air-pores, and all stomata whatever, are completely absent in roots. Of the other parts of the plant hardly one can be named on which they may not, at least in many cases, be observed[8].

[1] Pfitzer, Ueber d. Mehrschichtige Epidermis, &c., Pringsheim's Jahrb. VIII. *l. c.*

[2] Strasburger, *l. c.* Tab. 41, figs. 135-138, and our fig. 18, both of *Ficus elastica*.

[3] Von Mohl, Botan. Zeitg. 1849, Tab. IX; Chatin, Anatomie comparée des Végétaux, Plantes parasites, Tab. 80, 82.

[4] Chatin, *l. c.* Tab. 5, 6, 57, 58, 59, 64, 69, 70, 72, 77, 78, 87, 109, 110.

[5] Pfitzer, Pringsh. Jahrb. VII. p. 549.

[6] Duval-Jouve, Bulletin de la Soc. Bot. de France, XV. (1868) p. 139.

[7] Loew, de Casuarinearum caulis foliique evolutione et structurâ, p. 35.

[8] Rudolphi (Anat. p. 91) speaks of stomata on the anthers of *Lilium bulbiferum*; Unger (Exanth. p. 127) on those of *Capsella bursapastoris*, 'in a pathological state'; on the integument of *Canna*, Schleiden, Beitr. p. 10; also on the outer margin of the seed in *Tulipa*, Czech, Botan. Zeitg. 1865, p. 104.—They exist on Perianths, both with and without chlorophyll, in many

The chief place where they occur is the green leaf, surrounded by air, especially the leaves of land plants and floating water plants. Certain land plants destitute of chlorophyll, viz. Monotropa Hypopitys and Neottia Nidus avis[1], have no stomata at all. With the exception of the pistil Lathræa squamaria is without stomata[2]. On the contrary, on the leaf of Lathræa clandestina[3], as also of the Orobancheæ[4] and Lennoaceæ[5], they occur in considerable numbers, on that of the Cuscuteæ[4] at least here and there.

On Rhizomes[6] growing in the ground they are not uncommon, at least in isolated cases; e.g. the young potatoe before formation of the cork-layer[7], the tuberous stem of Herminium Monorchis[8], the rhizome of Epipogon, &c.

In parts which are submerged air-pores are as a rule completely absent, but here also exceptions occur. They are to be found regularly on the submerged primordial leaves and the germinal leaf of the Marsiliaceæ[9], on the submerged leaves of the Calitrichineæ, Sect. Eucallitriche[10]; Askenasy[11] found single ones on the cotyledons of Ranunculus aquatilis normally unfolded under water. The statement of H. Weiss on their occurrence on submerged parts of Najas and Potomageton is not confirmed.

In water-plants whose leaf can vegetate either submerged or in the air, as Ranunculus aquatilis, the Callitrichineæ, Hottonia, Myriophyllum, Marsilia, &c., the occurrence or distribution of air-pores varies according to the above-stated habit.

The air-pores occur (perhaps with exception of single cases of their solitary appearance on submerged parts) only where intercellular spaces, containing plenty of air, are present in the tissue covered by the epidermis. Still stomata are not always present where the latter is the case. Where tissue rich in air alternates with tissue with little or no air (Sclerenchyma, Collenchyma) there is as a rule in the epidermal tissue covering them a corresponding alternation of spots with and without stomata[12]. Connected with these are the universal phenomena of absence of stomata on the nerves of leaves; their occurrence near and between these, their absence on the channels and edges of channelled leaves, petioles, stems, and their presence in the surfaces, or furrows alternating with these; (e.g. leaves of Bromeliaceæ, Phormium, Grasses, stems of the Umbelliferæ, Equiseta, &c.: stomata-bearing bands and spots on the young shoots of Hedera, Juglans, Populus[13], on the sides, and at the

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plants, in others they are absent. Compare Rudolphi, Anatomie, pp. 85–91; Treviranus, Verm. Schriften, p. 50; H. Krocker, de Plantar. Epidermide (1833), p. 16: A. Weiss, Verhandl. Zool. bot. Vereins in Wien, 1857; and especially Hildebrand, Einige Beobachtungen aus der Pflanzen-Anatomie (1861).

[1] Rudolphi, Anatomie d. Pfl. (1807), p. 66.

[2] [Krause, Beitr. z. Anat. d. Vegetationsorg. d. Lathræa Squamaria. Diss. Breslau. 1879.] Bowman, Trans. Linn. Soc. London. XVI.

[3] Duchartre, Sur la Clandestine de l'Europe. Mém. de l'Institut de France, 1848.

[4] Unger, Exantheme d. Pfl. p. 49.

[5] H. Graf zu Solms-Laubach, Die Lennoaceen (Halle, 1871).

[6] Hohnfeldt Botan Zeigt. 1881, p. 38.

[7] Caspary, Botan. Zeitg. 1857, p. 117.

[8] Prillieux, Ann. sci. nat. 5 Sér. IV. p. 265, pl. 15.

[9] A. Braun, Monatsbr. d. Berlin. Acad. 1870, p. 665.

[10] Hegelmaier, Monographie der Gattung Callitriche, p. 10.

[11] Botan. Zeitg. 1870, p. 198.

[12] [Cf. Potonié, Beziehungen zw. d. Spaltöffnungsystem u. d. Stereom. b. d. Blatt-Stielen d. Filicineen, *Ref.* Bot. Centralbl. 1881. Bd. 8. p. 70.]

[13] Compare Trécul, Comptes rendus, tom. 73, p. 15.

base of the petiole of the Ferns (comp. below, Chap. IX). The occurrence of stomata in hollow depressions on the under surface of the leaf of many species of Banksia, and Dryandra [1] is a special case of the same thing, which derives its peculiar appearance only from the strong outgrowth of the nerves on the under side of the leaf. On the under surface of the leaf of Nerium oleander there alternate, between the nerves, spots with and without stomata. The latter occur in depressions of the leaf-surface, which are deep and narrow-necked, and covered thickly with hairs [2].

On the part or band, which bears stomata, the air-pores are besides in rare cases limited to circumscribed spots, separated by intermediate areas without stomata: the spots are then also characterised by a special form of the epidermal cells. Thus on the flat underside of the leaf of Saxifraga sarmentosa numerous stomata are collected in circular groups, removed some distance from one another [3]; on the under side of the leaf of many (but not all) Begonias, e.g. B. manicata, spathulata, Drègei, heracleifolia, two to six or more stomata stand side by side over a great common respiratory cavity [4].

As a rule there is over large surfaces and bands an almost uniform distribution of air-pores. Their number, both relatively to the number of the epidermal cells and to a definite superficial space, varies within wide limits according to the organ and species, and to some extent according to the condition of the surrounding medium. In the first relation we have, on the one hand, one stoma to almost every epidermal cell, e.g. in leaves of Monocotyledons, as Iris; on the other hand, as in the stems of many woody plants, Cuscuta, &c., there is one stoma to many hundred epidermal cells [5]. In the other relation, the maximum numbers found for $1^{mm}\square$ were 625 (under surface of leaf of Olea Europæa [6]), and 716 (under surface of the leaf of Brassica Rapa [7]). For most foliage leaves the number lies between 40 and 300, rarely higher or lower [8]. As above stated, on the stems of many woody plants the stomata lie several millemeters, or still further apart, as is conspicuously shown on the formation of lenticels of Sambucus, Acer, &c. (Chap. XV). A like stage of development being of course assumed, there may be laid down for each part of each species a definite average number, which is, it is true, liable to not inconsiderable individual variations. Karelstschikoff communicates examples of individual variation. On an equal surface (the same field of the microscope, which was not measured) six leaves of Viola tricolor, each taken from a different stock, had on the under surface between 21 and 43, the majority between 30 and 40; on the upper side 0 to 14, the majority between 9 and 13.

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[1] Von Mohl, Spaltöffn. d. Proteaceen, Verm. Schriften, p. 245.

[2] Amici, Ann. Sci. Nat. XXI. p. 438.—H. Krocker, *l. c.* p. 13.—Meyen, Physiol. I. p. 291.—Compare Pfitzer, Pringsheim's Jahrb. VIII. p. 49.

[3] Treviranus, Verm. Schriften, IV. 30.

[4] Viviani, Della struttura degli organ. element, tom. I. fig. 4, p. 151, quoted by Treviranus, Physiol. I. p. 466.—H. Krocker, *l. c.* p. 13, fig. 39.—Meyen, Physiol, I. p. 280, Tab. V.—On the development of the groups, compare Pfitzer, Pringsh. Jahrb. VII. p. 551.

[5] Compare the figures of Strasburger, Pringsheim's Jahrb. V; Hildebrand, Botan. Zeitg. 1870, Taf. I.

[6] Weiss, Unters. über die Zahlen- und Grössenverhältn. d. Spaltöffnungen. Pringsheim's Jahrb. IV. p. 124 ff.

[7] Unger, Anatom. und Physiol. p. 193.

[8] Compare Weiss, *l. c.*

Of the members surrounded by air, stems bearing chlorophyll are rich in stomata if leaves are absent: e.g. Equisetum, Salicornia, Casuarina, Colletia, Cactaceæ, &c. There are eighteen stomata on $1^{mm}\square$ in Cereus speciosus (Krocker). Leafy stems also, whose own foliage-surface is relatively very large, are rich in stomata, e.g. Campanula patula, linifolia, Salvia glutinosa, Polygonum aviculare, Vicia Faba, segetalis, Epilobium palustre, Capsella Bursa Pastoris, Möhringia trinervia, Linum catharticum, Potentilla aurea, and many others (Unger, Exanth. pp. 98–137). Unger ascribes numerous stomata to the green branches of ligneous plants, such as Vaccinium Myrtillus, Rhamnus cathartica, and Frangula. Morren found in Prunus Mahaleb 18, and in Rosa damascena 36 on each $1^{mm}\square$. Similar large numbers are found in related species, in Viburnum opulus, &c. (Stahl, Botan. Ztg. 1873, p. 578). In very many plants, on the other hand, very scattered stomata occur on the stems; e.g. in Prunus domestica seven, in Solanum tuberosum four on each $1^{mm}\square$, or still fewer; only in rare cases there are none at all.

From occasional observations on the petiole similar results are obtained as for the stem.

Numerous observations of their number and distribution have been made on the parts where they occur in largest numbers, viz. the laminæ of green foliage leaves of land and aërial plants. The older observations of Hedwig, Von Humboldt, Sprengel, the copious works of Rudolphi, and other more scattered notices, have been followed more recently by the works of H. Krocker, Unger, A. Weiss, E. Morren, Czech, and Karelstschikoff[1]. The very full statistics of Weiss inform us that of 157 species of land plants investigated, the mature foliage leaves have on an average on the space of $1^{mm}\square$

less than	40	stomata in	12	Species
40—100	„	„	42	„
100—200	„	„	38	„
200—300	„	„	39	„
300—400	„	„	12	„
550	„	„	1	„
more than 600	„	„	3	„

The distribution of the air-pores over the surface of the leaf is in land plants directly connected with that of the air-containing intercellular spaces. It differs therefore according as the leaf shows a bifacial or centric arrangement of the chlorophyll-containing parenchyma, and depends in individual cases upon the number and width of the lacunæ in this tissue. (Comp. Chap. IX.)

Herbaceous, flat, horizontal leaves with bifacial arrangement of the Parenchyma have usually stomata on both surfaces. Of 466 such species Karelstschikoff found this to be the case in 450. But of these 37 have on the upper surface only very few, often only solitary ones, lying near the nerves: and the majority are much poorer in stomata on the upper than on the under surface.

Firm, leathery, horizontal, also bifacial leaves, with smooth, shining upper surface, as

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[1] K. Sprengel, Anleitung z. Kenntn. d. Gewächse, I.—Unger, Exantheme der Pflanzen (1833). Anat. und Physiol. d. Pfl. pp. 193, 334.—Compare on the older literature, Meyen, Phytotomie, p. 108; E. Morren, Détermination des Stomates de quelques végétaux, Bullet. Acad. Bruxelles, tom. XVI (1864); Czech, Ueber Zahlenverhältnisse und Vertheilung d. Spaltöffnungen, Botan. Zeitg. 1865, p. 101; A. Weiss, Ueber die Zahlen- und Grössenverhältn. d. Spaltöffnungen, Pringsheim's Jahrb. Bd. IV; Karelstschikoff, Ueber d. Vertheilung der Spaltöffnungen auf d. Blättern, Bulletin Soc. Hist. Nat. de Moscou, 1866. For many details we must here refer to these works, which do not by any means coincide on all points.

Abies pectinata, Nerium, Rhododendron, Ilex, Ficus, Begonias, and many others, have stomata as a rule exclusively on the under surface: the same is the case with many firm herbaceous leaves, as in Glechoma hederacea, Asperula odorata, Trollius europæus, &c. (Karelstschikoff), Betula alba, Pirus communis, Carpinus, &c. (Morren). Rarely the relation is reversed, and with it the inner structure of the leaf also: there are herbaceous, and even leathery leaves (Pinus sylvestris and its allies, Eryngium maritimum L., &c.) with more stomata on the upper than the under surface; or with the upper surface exclusively bearing stomata, the under surface without them, as Pinus strobus, Thuja spec., Passerina hirsuta[1], filiformis, ericoides, and many Gramineæ with a deeply-grooved upper side of the leaf, e. g. Aira flexuosa, Calamagrostis epigeios, Stipa pennata, &c., which will be mentioned below. Flat leaves which stand vertically, and most fleshy juicy ones (Crassulaceæ, many Monocotyledons), bear stomata as a rule, though not without exception, on both sides; either they are equally numerous on both sides, or they preponderate on one side or the other. In this they answer to their centric structure. Leaves, which float on the surface of the water, have stomata exclusively on the upper side, or at least chiefly so, as Callitriche (Hegelmaier *l. c.*), the floating leaves of Sagittaria[2], Ranunculus sceleratus[3]. Further general rules, or laws for their distribution and their relations as to number, cannot for the present be laid down. No general decisive differences, either according to natural affinity and habit, or other conditions of structure of the epidermis, hold good throughout. Further, the proposition that, the more stomata there are on a surface, the less their size, and *vice versâ*, is not without exceptions. Of the observed cases of variation and conformity many cannot be referred directly to immediate adaptation. For instance, of the two Lathræas, above cited, which are of the same habit, with similar members and structure, the one has many stomata on stem and leaves, the other none.

But on the other hand, the occurrence and distribution of air-pores yields many remarkable examples of the change of structure by direct, often individual adaptation. This is especially the case for the amphibious water plants, and indeed all these, though they belong to the most different families and genera, as Marsilia, Sagittaria, Polygonum, Callitriche, Myriophyllum, Hottonia, Nasturtium, Ranunculus, show the same behaviour, viz. that where numerous stomata are found on surfaces developed in the air, corresponding surfaces developed under water have fewer stomata or none at all.

Marsilia quadrifoliata and other species of the genus[4] have, according as their habitat is submerged or not, floating leaves, with their upper side only exposed to the air and borne by thin delicate stalks, or leaves, borne on short stout stalks, rising into the air. These aerial leaves have on both surfaces almost equally numerous stomata, sunk slightly beneath the outer surface, between the strongly sinuous epidermal cells. In the floating leaves only the upper surface bears stomata, and on the same area of surface more than double as many as the aerial leaf. They lie between less sinuous epidermal cells (comp. above, p. 31), and in M. quadrifoliata, pubescens, diffusa, Ernesti, not depressed; in other species, as M. Drummondii, macra, they are depressed like those of the aerial leaves.

A similar difference exists between the aerial and floating leaves of Polygonum amphibium, and Nasturtium amphibium[5]. The petiole and laciniæ of the cut leaves of Ranunculus aquatilis, divaricatus, Myriophyllum, and Hottonia[6], which in their normal submerged state are without stomata, form numerous stomata when they develop in the air (Land form).

[1] Caruel, Nuovo giornale botan. Italiano, I. p. 194.

[2] Hildebrand, Botan. Zeitg. 1870.

[3] Ascherson, Botan. Zeitg. 1873, pp. 422, 631.

[4] Hildebrand, Botan. Zeitg. 1870. p. 1, Taf. 1.—A. Braun, Monatsber. d. Berlin. Acad. 1870, p. 670.—On the inconstant or exceptional behaviour of *M. Ægyptiaca* and some others, compare the same.

[5] Hildebrand, *l. c.*; Karelstschikoff, *l. c.*

[6] Askenasy, *l. c.*

Sagittaria sagittæfolia has stomata on both sides of the aerial leaves, 4–5 times as many below as above, on an equal area of surface[1]: on the floating leaves they are very rare on the under surface, but numerous above.—In the terrestrial forms of the Eucalli-triches the stem and both leaf-surfaces are rich in stomata[2], on the submerged forms they are absent on the stem, and occur only solitary on the leaves, on the floating leaves they are numerous on the upper side. A similar relation to that in Sagittaria occurs in the aerial, and the casually or abnormally produced floating leaves of Ranunculus sceleratus. An old statement of De Candolle, according to which leaves of Mentha developed under water have no stomata, is doubtful, and decidedly opposed by Rudolphi[3]. These facts are in accordance with the constant absence of stomata on certain submerged species, and their presence on closely-related, terrestrial species, e. g. in the genus Isoetes.

How far the finer gradations of distribution are directly caused by the mode of life and condition of vegetation requires careful investigation; in which, besides experimental treatment, it is important to compare, not, as has hitherto usually been the case, a large number of casually selected plants, but such as are closely related. By the latter method Pfitzer[4] has obtained the following result for a large number of indigenous grasses: that for these plants the number and distribution of the air-pores, together with the form of the surface and internal structure of the whole leaf, stand pretty generally in definite relation to the wetness of the locality. On both flat leaf-surfaces are numerous stomata in all marsh- and water-grasses observed (9 species, e. g. Phragmites communis, Alopecurus geniculatus): in numerous meadow- and weed-grasses (34 species, e. g. Alopecurus pratensis, Anthoxanthum odoratum, Hordeum murinum, Triticum repens): among the latter Festuca elatior is a remarkable exception, in that stomata appear only on the upper side of the leaf. Almost all grasses inhabiting very dry localities have leaves with well-marked longitudinal folds; the surface is therefore marked with long and narrow furrows, and the stomata are almost exclusively on the sides of the grooves of the upper side of the leaf (12 species, e. g. Aira caryophyllea, flexuosa, Elymus arenarius, Stipa pennata). Koeleria cristata and Agrostis vulgaris have, with leaf structure otherwise resembling the latter category, numerous air-pores also on the under side of the leaf. The remaining 14 investigated species inhabit bright glades, sunny hills and grass plots; they have leaves flat on both sides, and, like the above meadow-grasses, some of them have stomata on both sides (Avena pratensis, Holcus mollis, Phleum Boehmeri, Poa bulbosa, compressa, nemoralis, Milium effusum), others—perhaps, with exception of Triodia, plants which live only in shady situations—have them only on the upper side (Brachypodium silvaticum, Festuca gigantea, heterophylla, Melica nutans, uniflora, Triodia decumbens, Triticum caninum). Milium is an exception as compared with these.

Sect. 8. Numerous phanerogamic plants, of the most various adaptation, have usually besides the air-pores other stomata different from these, which may be called *Water-stomata* or *-pores*[5], since, under definite normal conditions, they serve as points of exit for excreted drops of water. These drops in many cases hold in solution large quantities of calcium carbonate, which dries into small scales. These differ accordingly from the air-pores by the slit (and the respiratory cavity below it) being, at least at times, filled with water. They are further characterised, as far as investigations extend, by their guard-cells being immovable, that is, they are incapable of independent intermittent widening. In many cases this is beyond

[1] Karelstschikoff, *l. c.* [2] Hegelmaier, *l. c.*
[3] Anat. d. Pfl. p. 69. [4] *l. c.* Pringsheim's Jahrb. VII.
[5] [Cf. Langer, Botan. Zeitg. 1879, p. 511.—Gardiner, Quart. Journ Micr. Sci. 1881, p. 407.]

doubt, since here the guard-cells die off at an early stage (e. g. Tropæolum, Colocasia, Aconitum, &c.), or disappear altogether (Hippuris, Callitriche); other cases certainly require confirmation. Finally, there is often besides this a considerable difference of form and size from the air-pores, which sometimes occur on the same epidermal surface with them.

The water-pores always lie over the ends of the vascular bundles, the structure of which is described in Chapter VIII; and therefore usually near the margin of the leaf, on the teeth, and, in most known cases, on their upper side: more rarely on other parts of the leaf-surface, singly or in groups, in the latter case often between epidermal cells, which differ from the rest in special form and (smaller) size. Also in closely related species there is, according to the species, in one case a single pore, in another a group of pores. The higher their number at one place, the smaller on the average is their absolute size, and also the difference in size between them and the air-pores connected with them. The absolute size is in extreme cases very considerable, by far exceeding the maxima for the air-pores.

According to their shape, one can distinguish two extreme forms of water-pores; on the one hand those with almost semicircular guard-cells, and with a slit always quite small and *short* (Crassula, Ficus, Saxifraga); and on the other hand those with a very large, *long* slit which is always found open, e. g. the huge stomata on the leaves of Aroideæ, Papaveraceæ, and Tropæolum. The largest of the latter are not uncommonly examples of the early death of the guard-cells previously mentioned.

The occurrence of water-pores is a very widespread phenomenon, to which the not very lucid statement of Trinchinetti on 'Glandulæ periphyllæ' refers[1]. Recently Mettenius[2], and after him Rosanoff[3], Borodin[4], and Magnus[5], have paid especial attention to them.

The form with relatively *longer* slit is known among land plants in the case of the water-dropping apices of leaves of the Aroideæ; in Colocasia antiquorum[6], Caladium odorum[7], and C. esculentum[8], there are two or three enormously large, wide, open pores. The water-dropping spot on the middle of the under side of the hair-like leaf-apex of Richardia æthiopica has numerous widely open stomata, which are larger and rounder than the air-pores. Further, of Dicotyledons, the following cases, mostly on the authority of Mettenius, are to be mentioned.

One relatively very large, wide, open pore is to be found at the apex of the leaf-teeth of the Fuchsias (Fuchsia globosa, &c.), Primula sinensis (rarely 2), (comp. below, Chap. VIII); on the upper side of each tooth (and of the apex of the leaf) in Saxifraga orientalis, cuscutæformis, punctata, Heuchera, Mitella, Soldanella Clusii, Primula auricula, marginata, acaulis, species of Aconitum and Delphinium, Eranthis; *one or two* in the same position in Sambucus nigra, Valeriana sambucifolia, Doronicum Pardalianches, Ribes triste, Prunus Padus; *three* in Cyclamen; a group of 3–6 of them in the same position in Ulmus campestris, Carya amara, Cratægus coccinea, Helleborus niger, Geranium macrorhizum; of 6–8 in Crepis sibirica, Helenium autumnale, Verbesina virginica; an about equal, but not quite definite, number of them at the same point in

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[1] Linnæa, Literaturblatt, pp. 11, 66.
[2] Filices horti Lipsiensis, pp. 9, 10.
[3] Botan. Zeitg. 1869, p. 883.
[4] Ibidem and 1870, p. 841.
[5] Botan. Zeitg. 1871, p. 479.
[6] Duchartre, Ann. Sci. Nat. 4 Sér. tom. XII. p. 264, pl. 17.
[7] E. de la Rue, Botan. Zeitg. 1866, p. 321.
[8] Mettenius, *l. c.*

Hieracium sabaudum, Eupatorium verticillatum, Platanus occidentalis, Corylus Avellana, Claytonia linoides, Escallonia spec., Aralia racemosa, Ferula tingitana. A numerous group of pores is to be found at like points in Tommasinia verticillaris, Archangelica officinalis, Smyrnium perfoliatum, Heracleum flavescens, Eryngium planum, and other Umbelliferæ; Cerastium glabratum, Geum agrimonioides, Aremonia, Potentilla Thuringiaca, and

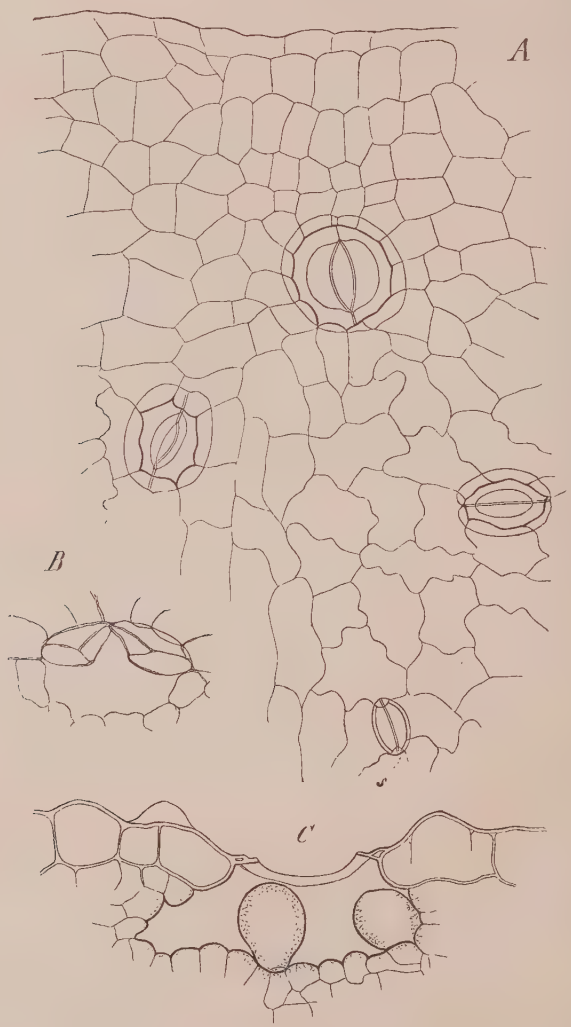

FIG. 19.—Tropæolum Lobbianum; upper surface of leaf. *A* (150) epidermis, from the margin, over the end of a strong vascular bundle, with three large water-pores; *s* air-pore. *B*, *C* perpendicular section through water-pores and their immediate vicinity (250). In *C* some of the cells surrounding the wide respiratory cavity have grown out into large papillæ rising into the cavity.

other species; Alchemilla vulgaris, Ranunculus lanuginosus, and other species; Physostegia virginica, Lycopus exaltatus, Hieracium Pilosella, denticulatum (apex of leaf), Rudbeckia speciosa, Senecio vulgaris, and other Compositæ; Valeriana Phu., Brassica spec., &c. In the examples given, the upper side of the leaf has air-pores also. Galium

Mollugo and Rubia tinctorum have practically no air-pores on the upper side, at the apex they have a group of water-pores.

In Papaver orientale, somniferum, and other species, 2–3 large pores lie in a small cowl-like depression on the under side of the teeth of the leaf.

Tropæolum majus, Lobbianum and other species have over each nerve-ending at the margin of the peltate leaf one very large water-pore, near this 2–3 or 4–5 (Tr. Lobbianum) additional ones which are rather smaller (Fig. 19). I have not found the pores described by Mettenius and Rosanoff on the callous middle portion of the leaf. Nelumbium speciosum has a group of several pores in the last-named spot.

Among submerged water plants we know from Borodin that in Callitriche verna one large open pore lies over the end of the vascular bundle, on the upper surface of the leaf. In Callitriche autumnalis there lie at the same spot on the young leaf a group of 3–8 open stomata; in the mature leaf the guard-cells of these break down, so that there remains a wide hole in the epidermis. In Callitriche verna also this phenomenon appears in the older leaf: nevertheless I found the guard-cells still intact on leaves several months old. The apices of the leaves of Hippuris behave similarly to those of Callitriche autumnalis (Borodin). On the segments of the young submerged leaves of Ranunculus aquatilis, divaricatus, Hottonia palustris, Askenasy[1] found several stomata, which die off with the whole apex before the complete maturity of the leaf. It is doubtful whether these belong to the category in question.

Water-pores with a *short* slit are known in the case of a number of species of Crassula, and Rochea and many species of Saxifraga and Ficus with depressions on their leaves.

The leaves of the above Crassulaceæ[2] have round spots or depressions easily seen with the naked eye, either on both surfaces (Crassula portulacea, Lam., arborescens, cultrata, tetragona, lactea) or only distributed on the upper side (C. cordata, perforata); or forming a row just within the margin of the leaf, either on both surfaces (C. lactea, ericoides, Rochea coccinea), or only on the under surface (C. lycopodioides, L., C. spathulata), in the latter, one at the base of each notch between two teeth. An ending of a vascular bundle expands beneath the epidermis covering the depression. Scattered between the small, delicate cells of the latter lie, in most species, several (5–8, in C. lactea up to 25) stomata with short slits, which are smaller than the air-pores of the same leaf. In C. perforata and Rochea coccinea (Fig. 20, comp. also below, Chap. VIII) the whole depression consists of *one* stoma, *exceeding* the air-pores in size, and somewhat sunk. The air-pores are present in most species in large numbers between the large cells of the epidermis of both surfaces of the leaf. In C. cordata they are absent from the upper side, which alone bears depressions.

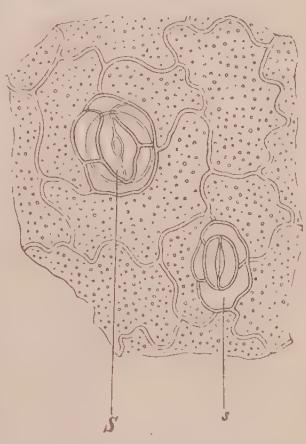

FIG. 20.—Rochea coccinea; small piece of epidermis from margin of leaf. *S* water-pore; *s* air-pore, with subsidiary cells. The scattered spots are wart-like outgrowths of the outer wall.

The leaves of the Saxifrages of the division Euaizonia have depressions on the notches of their margin, those of the division Kabschia (Engler) and Porphyrion on their upper side. In these depressions lime is excreted always, or at least while the leaf is young. The base of these, towards which an end of a vascular bundle runs, is constructed similarly to the spots in Crassula, delicate and small-celled epidermis with two (S. crustata), or 2–4 (S. Aizoon, longifolia, Rocheliana) large stomata, or one large stoma (S. retusa, oppositifolia, cæsia) forming the base of the depression.

[1] Botan. Zeitg. 1870, p. 235.

[2] Magnus, *l. c.*

The depressions on the upper surface of the leaf of some species of Ficus (F. neriifolia, diversifolia, Porteana, Cooperi, eriobotryoides, leucosticta, &c.) have in the main the same structure as in Crassula.

The openings which Trécul[1] describes on the large prickles on the leaf-nerves and petiole of Victoria regia may be here supplementarily mentioned, being doubtful as regards their structure, and requiring further investigation. These prickles enclose a thin vascular bundle, which ends under their apex, and at the apex itself is to be found a depression with one circular opening (ostiole).

Finally, while referring to later chapters, it must be remarked that the excretion of water or solutions of lime over the ends of vascular bundles is not always connected with the presence of water-pores.

Sect. 9. Gaps in the epidermis other than stomata and their modifications occur normally only in rare exceptional cases. In connection with the water-pores there may here first be mentioned the cracks, which occur regularly at the apex of leaves of the grasses (seedlings of Zea, Secale, Triticum, &c.); from these drops of water are expressed. They arise by irregular tearing of the originally cowl-like apex of the leaf, when this spreads itself out flat as it unfolds. Gaps of another sort, as found by Milde and King[2], occur on the middle part of the winged base of the leaf of Osmunda regalis, cinnamomea, Claytoniana, Todea rivularis, and on the ligule of the base of the leaf of Isoetes lacustris. The undulating lateral walls of the epidermal cells leave intercellular spaces between them, which are elliptical or circular in surface-view, and are often as large as the cells themselves. Their distribution is irregular: often many are near one another, even two between two cells, often there are none for a width of several cells. They pass through the entire thickness of the epidermis, and open into the intercellular spaces to be found below them. They are filled either with air or with a colourless jelly of unknown origin.

No further examples can be here adduced of gaps in the epidermis, which are not to be classed with stomata; mistakes formerly made with regard to Salvinia and Azolla have been corrected; the supposed round pores of the Pleurothallideæ, again reproduced by Unger[3], have been proved to be the insertions of sunken hairs[4]; and Luerssen has recently shown that the large pores, visible with the naked eye in the leaf of Kaulfussia, are typical stomata, of huge size and wide cavity, with collapsing guard-cells, and surrounded by 2–3 rings of subsidiary cells[5].

Sect. 10. Such outgrowths above the outer surface of the epidermis as do not belong to the cell wall alone are termed, in the plants with which we are concerned, *Hair-structures* (*Trichomes*, *appendages of the Epidermis*). These spring from cells of the epidermis, and are derived from them.

We may distinguish as typical forms of hair-structures, *Bladders* (Papulæ), *Hairs* (Pili, Setæ), *Scales* (Squamæ, Lepides, and Paleæ), and *Shaggy hairs* (Villi), *Warts*, and *Prickles*. These forms are characterised by simple relations of shape, which mostly explain themselves according to their meaning borrowed from the language of ordinary life, and by equally simple differences of structure: *Bladders*

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[1] Ann. Sci. Nat. 4 Sér. I. 156, p. 13, fig. 10.

[2] Milde, Monogr. generis Osmundæ, p. 86.

[3] Anat. und Physiol. p. 194.

[4] Meyen, in Wiegmann's Archiv, 1837, I. p. 419; Schleiden, ibid. 1838, I; Beitr. p. 5.

[5] De Vriese et Harting, Monogr. des Marattiacées, p. 14, Taf. V. D.—Luerssen, Botan. Zeitg. 1873, No. 40.

are isodiametric, usually unicellular bodies; *Hairs* are sac- or thread-like bodies, unicellular, or consisting of a row of cells, simple or branched; *Scales* are flat membranous structures, always consisting of many cells, arranged in one or several layers; *Shaggy hairs* are thread-like bodies, consisting of two or many layers or rows of cells; *Warts* and *Prickles* are of similar constitution, but are not thread-like, but massive and hard, the warts are blunt, the prickles pointed. Intermediate forms and combinations of these types are common, and may of course be easily named after them.

On each hair-structure may be distinguished the body and the foot. The former is the part which protrudes outwards above the epidermal surface. The foot is the part which lies within this; it is rarely similar in form to the epidermal cells, especially often it exceeds them in height, as it not uncommonly extends inwards far beyond the inner surface of the epidermis, into the sub-epidermal tissue.

The epidermal cells, which surround the foot, may resemble those not bordering on a hair; very often they are quite different from these, and may then be termed *subsidiary cells* of the hair. Of the various forms of these, that of an annular or rosette-like girdle of subsidiary cells surrounding the foot of the hair recurs especially often (Fig. 21 *B*).

Around the foot of many hairs, or below it, the subepidermal tissue, covered by the epidermis, bulges outwards, so that the foot is borne by an *emergence* of that tissue. This may be limited to a slight excrescence, upon which, as its 'bulbus,' the hair is seated, or to a small, stalk-like outgrowth, which in multiseriate shaggy hairs is with difficulty distinguished from the hair itself; but, on the other hand, it may attain considerable dimensions, as in the prickles of Dipsacus[1], and species of Solanum, &c., which bear a hair on their apex, or the fringed scales of Begonia manicata[2].

The converse condition of the origin of a hair, in a more or less deeply hollowed depression of the surface, is not less common.

Small hairs do not always overtop the edge of the depression in which they stand. They fill it completely, or only partially, as those on the leaves of the Pleurothallideæ (Pleurothallis, Stelis, Physosiphon, Nephelaphyllum, Octomeria), which (comp. page 54) were wrongly described by Meyen as cavities of the Epidermis.

The direction of the body of the hair, as regards the surface which bears it, varies extremely between that at right angles and that parallel to it.

The hair-structures of one and the same surface are in the minority of cases all alike, if slight individual differences be disregarded. As examples may be named all known cases of Root-hairs, Leaf of Elæagneæ, Bromeliaceæ, Leaf and stem of Convolvulus Cneorum, &c. Much more commonly one and the same surface bears hairs of different properties, two to five sorts often occurring close to one another. Comp. Fig. 21.

If we disregard the root-hairs, which with very few exceptions (Elodea, Lemna, Ophioglosseæ) are universally distributed, and reproductive organs, which are not to

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[1] Schleiden, Grundz. 3 Aufl. I. p. 281.

[2] Compare Weiss, in Schr. d. zoolog. bot. Vereins. Wien, 1858.

be specially noticed here, some few families are distinguished by complete or almost complete absence of hair-structures, as the Equisetæ, the Coniferæ, the Potameæ, and Lemnaceæ.

They occur in the majority of genera and species, though certainly to a very variable extent.

Different vegetative adaptation does not determine the presence or absence of hair-structures; they occur under all states of adaptation, even in submerged species, as Callitriche, Nymphæa, and species of Ranunculus. On the other hand, their number and development seems certainly to be influenced by the nature of the environment, since observation shows that in allied species, and in individuals of the same species, the hairiness increases with the sun-light, dryness, and airiness of the spot. But there is no safe foundation for a definite assertion on this point.

As regards the distribution of single *forms of hairs* through families and genera, the case is similar to that of the forms of foliage leaves. On the one hand there is great uniformity of the majority of species and genera of one family, at least as regards *one* characteristic form of hair, so that one may speak, for instance, of the bristles of the Borragineæ, the short (glandular) capitate hairs and scales of the Labiatæ, the stellate hairs of the Cruciferæ, the tufted hairs of the Malvaceæ, the multiseriate shaggy hairs of the Melastomeæ, the delicate branched hairs accompanying the capitate hairs of the genus Lavendula, the three characteristic forms of hair of most of the Hieracia, &c. On the other hand, in natural families (e.g. Compositæ, Labiatæ), and even genera (e.g. Solanum), the most various forms exclude one another; or one characteristic definite hair-form recurs on corresponding parts in the most remote genera and families, as the stinging hairs on the leaf of Urticaceæ and Loaseæ, the shield-like stellate hairs or scales on those of the Oleaceæ, Elæagneæ, and species of Solanum, Croton, Bromeliaceæ, and Ferns; the spindle-shaped, appressed hairs, with central attachment of the Malpighiaceæ and Cruciferæ, &c.

The development of hair-structures, both uni- and multicellular, begins, in all certainly investigated cases, from *one* epidermal cell, as *Initial cell*. This cell protrudes beyond the outer surface of those surrounding it: the part within this surface develops into the foot, the protruded portion into the body of the hair. The growth which ensues is, according to the special case, acropetal, basipetal, or intercalary, as regards the hair itself (Rauter). It is obvious that in forms consisting of more than one cell, divisions accompany growth, and the successive division-walls appear in definite number and position for each case; further, that the definite form and articulation depend upon the successive divisions, and the growth of the cells after the division is complete. In 2- to 4-seriate shaggy hairs, scales, &c., in which the rows of cells are continuous into the foot, and are there represented by two or many cells side by side in the epidermis, e.g. Hieracium aurantiacum and its allies, division of the initial cell perpendicular to the epidermal surface begins almost simultaneously with, or very soon after the protrusion of the body outwards. The development of an emergence bearing a hair begins later than the origination of the hair itself by local growth of the subepidermal meristem, and of the epidermal cells surrounding the initial cell of the hair.

The origination of the hair-structures begins on stem and leaf at a very early age, on the former however, as a rule (but not always), not above the point of insertion of

the youngest leaf[1]. On the same surface, their formation begins at an earlier stage of development than that of the stomata. 'The succession of appearance of the hair-structures follows the development of the part of the plant which bears them, but not so thoroughly that the hairs, in their successive appearance, arrange themselves exactly according to the direction of the advancing growth of the leaf which bears them. Not uncommonly new hairs grow out between those already formed.' Most hairs on the parts named attain their full development with or before the complete unfolding of the bud. The thick covering of hairs, scales, and shaggy hairs in the bud-condition, is generally known. As the bud unfolds, the thickness of the covering decreases, partly as a result of the separation of the persistent hairs on the growing surface; but partly through the disorganisation of hairs present in the bud during the unfolding, so as to leave behind only rudiments on the unfolded parts, or hardly that[2]. Even parts, which after unfolding are completely bare, may be hairy in the bud, e. g. the leaves of Ficus elastica[3]. (Comp. Fig. 18 *A*, p. 44.)

We may accordingly distinguish between *evanescent*, *transitory* hairs which are *peculiar to the bud*, and *persistent* hairs. Among the latter we may again distinguish, as will be shown below (Sect. 13), between such as persist as *living* hairs, and others which are adherent but *dry*.

In roots the case is different from that described. It is a universal rule, that here the hairs always appear on that part which is just ceasing to unfold, i. e. to extend.

The above sentences will give the general points of view for the anatomical consideration of the differentiation of the hair-structures. Under this head are ranged structures rich in peculiarities, which have been the object of many works, and therefore have a huge literature to show. In older times more especially the forms, articulation, and functions of the hairs, which do not here concern us, were dealt with[4]; in more recent, and the latest times, investigations on the history of development are considered of more importance[5]. I cite below for the time up to 1867 only the chief works, and

[1] On this fact, which need not be further noticed here, compare Hofmeister, Die Lehre von der Pflanzenzelle, pp. 411, 545, and Rauter, Entwickl. einig. Trichomgebilde, p. 33. [Further, cf. Von Höhnel, Botan. Zeitg. 1882, p. 145.]

[2] Compare Hanstein, Botan. Zeitg. 1867, p. 697 ff.

[3] Schacht, Abhandl. d. Senckenbergischen Gesellsch. I.

[4] Guettard, Memoires sur les glandes des plantes, &c. Eleven treatises in the Mémoires de l'Acad. Royale des Sciences, Paris, 1745–1759; altogether 560 quarto pages. Compare A. Weiss, *l.c.*—F. v. P. Schrank, Von den Nebengefässen d. Pflanzen, Halle, 1794, 8vo., with 3 plates.—Rudolphi, Anatomie, p. 117 ff.—P. de Candolle, Organographie végétale, I. p. 108.—B. Eble, Die Lehre von den Haaren in der gesammten organ. Natur. Bd. I, Wien, 1831 (only known to me from references).—Meyen, Secretionsorgane d. Pflanzen, Berl. 1837.—Physiologie, Bd. I and II (1838–1839).—Bahrdt, De pilis plantarum, Diss. inaug.; Bonn, 1849.—A. Weiss, Die Pflanzenhaare (Abdr. aus Karsten's Botan. Untersuchungen, Bd. I); 306 pages, 13 plates, 8vo.

[5] Hanstein, Ueber die Organe der Harz- und Schleimabsonderung in den Laubknospen. Botan. Zeitg. 1868.—J. Rauter, Zur Entwickelungsgeschichte einiger Trichomgebilde; Wien, 1871, with 9 plates (from Denkschr. d. Wiener Acad. Bd. XXXI).—J. Martinet, Organes de sécrétion des végétaux; Ann. Sci. Nat. 5 série, tom. 14 (1872), pp. 91–232, pl. 8–21.—O. Uhlworm, Beitr. z. Entw. der Trichome, Botan. Zeitg. 1873.—Further, N. Kauffmann, Ueber die Natur der Stacheln; Bullet. Sci. Nat. de Moscou, tom. XXXII. p. 301 (1859); Warming, Sur la différence entre les trichomes et les epiblastèmes d'un ordre plus élevé (Abdr. aus Kopenhagen. Videnskab. Meddelelser), Copenhague, 1873.—C. Delbrouck, Ueber Stacheln und Dornen. Diss., Bonn, 1873.—S. Suckow, Ueber Pflanzenstacheln, etc. Diss., Breslau, 1873. [Further, Reinke, Anatomie d. an Laubblättern vorkommenden Secretionsorgane, Pringsheim's Jahrb. X. p. 119.]

refer for the complete enumeration of them to the works quoted, especially those of Weiss and Martinet.

In face of the various facts and opinions it is our first business to determine what one understands by hair-structures or Trichomes. There are two opposed opinions on this point. The advocates of the one apply this name only to outgrowths belonging to and derived from the epidermis—in the sense indicated in Sect. 1—; others apply it to all characteristically formed outgrowths of the plant, to which the conceptions or traditional terms stem, leaf, root cannot be applied, whether these protuberances belong to the epidermis alone, or whether the subepidermal cells, and even the vascular system take part in their formation, e. g. the prickles of the Roses, of species of Smilax and Solanum, and of the Thorn-apple, &c. The foundation of the latter view seems to me to lie less in observable facts, than in the historical fact that outgrowths such as prickles and warts were formerly included among hair-structures, since it was thought that they belonged to the Epidermis[1]. If we deviate from this view, which is now proved to be incorrect for the majority of cases, the term trichome must also be restricted, and all outgrowths must be excluded from it, which include in themselves more than epidermis. Otherwise a quite unnecessary confusion would be brought into well-founded views and relations, since, if one includes among trichomes all outgrowths of the surface of stem or leaf, one must also include those of the *leaf margin*, i. e. all leaf-teeth. If we adhere to the anatomical and developmental facts which are clearly before us, we easily obtain the definition here given of the idea of the hair-structure or Trichome as equivalent to an outgrowth of the epidermis, and the distinction of this from those outgrowths in which more than the epidermis takes part, for which the term *Emergences* proposed by Sachs (Textbook, 2nd Eng. Ed. p. 161) is suitable.

The distinction between hairs and peculiarly formed epidermal cells may present difficulties in many single cases, e. g. in the genus Mesembryanthemum, where large cells scattered in the epidermis bulge outwards in M. crystallinum as huge bladders, while in other species they scarcely rise above the surface. But it is just the same whether one calls them hairs or not. The case, described by Uhlworm (*l. c.*, Fig. 28–30), for the warts of Gunnera scabra, which are covered by a piece of epidermis consisting of cells elongated perpendicular to the surface, may be denoted, as above, or one can speak of a group of laterally-united prismatic unicellular hairs, or one may (with Uhlworm) term the whole piece of epidermis a multicellular trichome, which in that case forms an exception from the rule of the origin of each trichome from *one* initial cell.

Starting, as is always necessary in defining types, from clearly characterised forms, the above established leading types of hair-structure may easily be separated according to their external development, and they are as a rule easily distinguished, without very exact investigation, by habit and consistency. Their distinction is therefore to be recommended for use in systematic Botany, which has as yet made use of these relations less than they might be employed. Intermediate forms are by no means absent. But these may easily be subordinated, or appended to the types. It is however often indifferent to which of the types a special case is appended, and this is defined as convenience may dictate. One may, for instance, call the flat horizontal appendages of the Elæagneæ, or of Polypodium Lingua, stellately branched, multicellular hairs, just as well as stellate scales; or a capitate hair with a large compound head may just as well be termed a long-stalked scale or a dermal wart.

Within the main limits, special forms are incredibly various as regards form, special articulation, and direction, &c. The detailed description of them is the subject of the most special systematic study, and their minute classification, though it might have a significance at the times of Guettard and Schrank, can only be idle play at the present time. Here, therefore, we may give only a few details and one or two drawings

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[1] Compare *e.g.* Schleiden, Grundz. 3 Aufl. I. p. 271; Unger, Anat. und Physiol. p. 188.

(Fig. 21) as examples of the leading forms, and for further information refer to the literature above cited, or to any handful of plants.

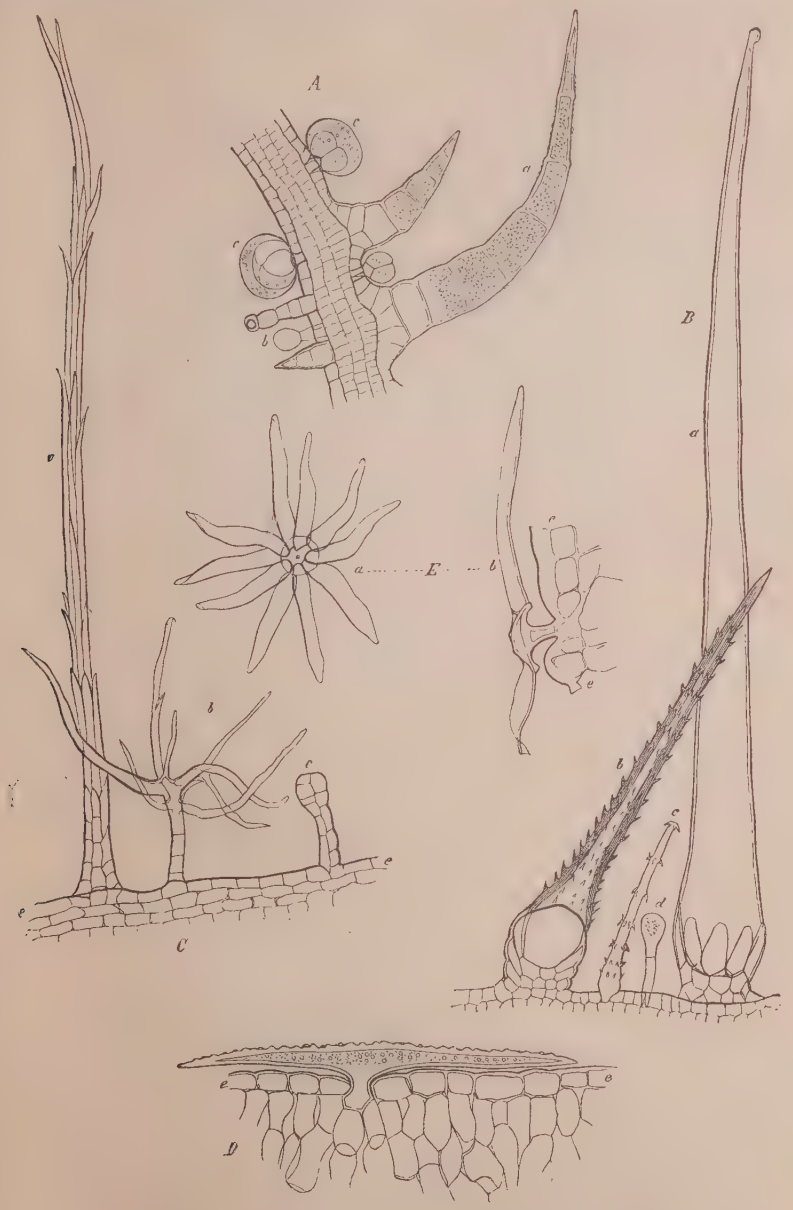

FIG. 21.—Examples of forms of Hairs. *A* transverse section through a young leaf of Plectranthus fruticosus. *a* conical multicellular hairs, *b* small capitate hair, *c* short glandular capitate hairs (150). *B* Cajophora lateritia; transverse section through the carpel; explanation in the text (150). *C* Hieracium piliferum; leaf, longitudinal section. *a* thread-like, *c* short capitate shag-hair; *b* multicellular hair, with irregular stellate terminal cell (90). *D* Cheiranthus cheiri; under-surface of leaf, longitudinal section. Explanation in the text (150). *E* Polypodium lingua; under-surface of leaf. Stellate hair, *a*, in surface view (90); *b* transverse section (150).

I. Hairs, elongated cells or rows of cells, simple or branched. Free ends not much widened, or tapering conically: *Filiform and conical hairs;* or widened into a head, *Capitate hairs* (*Pili capitati*). In the latter case the head is often articulated as a cell-surface, or cell-body; these are transitions to the leading forms II and III, and may be named according to convenience.

1. *Filiform and conical hairs.*

(*a*) *Unicellular and unbranched* forms belonging to this group arise, by the arching outwards of the whole or part of the outer wall of one epidermal cell, so as to form a cylindrical or conical protuberance above the neighbouring surface. The whole hair is a single cell, of which a sac-like part of variable size protrudes as the body, the rest is embedded in the epidermis as the foot.

To this type belong all root-hairs. They are as a rule partial protuberances of the outer wall of one epidermal cell; when freely developed they are bluntly cylindrical, but by application to the solid particles of soil they assume irregular forms and curvatures[1], rarely they are branched (in Brassica Napus observed by Sachs, Textbook, 2nd Eng. Ed. p. 100), or they may arise in pairs from one epidermal cell. Only in Lycopodium[2] can special hair-cells be distinguished from the other epidermal cells on the root. From many of the original similar polyhedral cells, a part of the lower end is cut off by an oblique wall as a small cell, which divides further into 2–4 cells: each of these grows out into a hair: the hairs therefore in the mature root are arranged in groups between the elongated epidermal cells.

On the foliage-leaf are to be found innumerable further examples. As a remarkable form may be mentioned the conical hairs of many Borragineæ, Loaseæ (Fig. 21, *B*), Hydrophylleæ (Wigandia), Urticeæ, many Cruciferæ, Biscutella, Draba aizoides, Sinapis, Brassica spec.), also of Iatropha urens, and napæifolia. In the stronger forms of this category, whether they sting or not, the base of the conical hair is swollen, and encroaches on the surrounding tissues. It is usually borne on a more or less protuberant emergence, and is surrounded by a rosette of peculiarly formed subsidiary cells. To certain of these hairs (Loasa, Nettles, Iatropha spec.), which are characterised as a rule by a button-shaped rounding-off of the upper end, and by the nature of their walls and contents (Sect. 13), but by no further anatomical peculiarities of the hair itself or its surroundings, the name *stinging hairs* (Stimuli) has been given. Compare the figures of Meyen (Secretions-organe), Weiss, Martinet, and Rauter, and the more or less successful figures of the stinging-hairs of the nettle in most text-books. Forms of this nature are especially various in the Loaseæ (Loasa bryoniæfolia, Cajophora lateritia). On the leaf and the carpels of the latter (Meyen *l. c.* Tab. VIII, *B* in our Figure 21) are seated two sorts of conical hairs borne by slight emergences, and with their swollen bases surrounded by subsidiary cells, (1) long, smooth, blunt, stinging hairs (*a*), and (2) shorter ones, having the point oblique to the surface, with a thicker wall and numerous whorls of short points turned upwards (*b*); further (3) small thin hairs, with a circle of reflexed spicules at the blunt end, and many such laterally, these have a tapering base inserted in the epidermis (*c*): lastly (4) small 2– to many-celled capitate hairs (*d*).

The term *unicellular branched* hair may be applied to those described second in Cajophora (Fig. 21, *b*, also *c*), inasmuch as the spicules or little hooks are short branches. Transitions from the unbranched to the branched form are to be found in the Cruciferæ; in Draba aizoides, D. hispanica, Boiss., side by side with the above-named simple conical hairs, occur others which, though otherwise of like character, are once branched at an acute angle. More richly branched hairs, with many modifications and complications, are the prevailing form for the leaf of most Cruciferæ, though they are not exclusively present. The body of these unicellular branched hairs rises from the expanded foot. After a short distance, through which it remains undivided, it splits into 2–4 equal

[1] Sachs, Exp. Physiol. p. 186.

[2] Nägeli und Leitgeb, Bau und Wachsthum der Wurzeln, p. 124.

diverging branches, which may themselves be repeatedly forked—often, as in Matthiola arborescens, with cymose unequal continuation of the successive forked branches. In the forms that are felt-like to the touch, as Farsetia incana, Matthiola arborescens, Alyssum petræum, Draba spec., the branches rise obliquely from the epidermis upwards. In others they are parallel to the epidermis, and lying close to it they spread out like a flat star: stellate hairs, e. g. Capsella bursa pastoris, with 2–4 simple rays, Alyssum petræum, with 3–4 rays once or twice dichotomised. If the body of the hair divides close above the outer surface of the epidermis into two conical limbs, both of which are directed in one line parallel to the surface, the form is attained of a spindle lying parallel and close to the epidermis; this at its middle passes over into the foot, which is inserted in the epidermis. Such spindle-hairs, with their longer axis as a rule parallel and close to the part which bears them, are characteristic for Cheiranthus cheiri (Fig. 21, *D*) and Erysimum canescens; they are also to be found among 3–4 rayed stellate forms in Capsella, Erysimum cheiranthoides, &c.

Similar forms occur in other families: unicellular, appressed, very regular stellate hairs, with sharply conical, short, undivided rays, e. g. on the leaves of Deutzia scabra, 3–6 rayed on the upper, usually 9–10 rayed on the under surface.

In the Malpighiaceæ[1] there is a similar series of forms, though these are less various than those in the Cruciferæ: simple erect conical hairs, and forked, stellate, and spindle-shaped hairs. The erect branched hairs are simply two-forked, with equal or very unequal branches; many-rayed stellate hairs occur in the genus Thryallis; specially large and remarkable, but otherwise of fundamentally similar form to those of Cheiranthus, are the unicellular appressed spindle-hairs in this family which are termed by de Candolle (Organogr. p. 103) Malpighiaceous-hairs.

Another often-described case of the last-named form are the spindle-hairs ('climbing hairs') of Humulus lupulus, with their ends curved like a hook, and borne on an emergence. Further, Weiss (*l. c.* p. 528) mentions similar appressed spindle-hairs for 'many species of Galega, Astragalus, Acer, Verbena, and Apocynum.'

(*b*) Most conical and filiform hairs are *multicellular*. In the simplest case they are two-celled, so that *one* transverse wall separates a foot-cell from one cell of the body; in other cases they consist of more, and even numerous cells (Fig. 21, *A a*). As regards the form, the same forms appear again, as in the unicellular hairs. One may even say that the same hair may be uni- or multicellular, i. e. that the formation of transverse walls is of minor importance; thus the long conical hairs on the leaf of Pelargonium zonale are sometimes unicellular, sometimes they have 1 or 2 transverse walls; in the latter case they are somewhat thicker-walled than in the former. Unbranched, multicellular, filiform, and conical hairs are the commonest form of all. Examples: leaf of Cucurbitaceæ, Solanum tuberosum, and its allies; most Labiatæ (Stachys, Salvia, Thymus, Plectranthus, and others, but not all genera); many Compositæ (Helianthus, Cnicus, &c.); Tradescantia spec.; the huge yellowish-brown hairs, up to 3 cm. in length, on the base of the leaf of several species of Cibotium, which appear in the shops as Pingawar Djambi, Pulu, &c.[2]

Among the branched forms, in the first place, those described under the unicellular hairs recur as pluricellular. Hairs of the form of a T, that is, stalked spindle-hairs, with pluricellular stalk and unicellular cross-piece in the Anthemideæ (Pyrethrum roseum, Tanacetum Meyerianum Sz., Artemisia absinthium, A. camphorata, according to Weiss, *l. c.*). Stellate hairs with unicellular, often rather irregular star, or even two stars, one above another, on a pluricellular stalk: Hieracium Pilosella and its allies. (Fig. 21, *C b*, comp. Weiss, Rauter, *l. c.*)

Polypodium lingua has stalked, umbrella-shaped, very regular stellate hairs, in which the foot, the erect stem, the centre, and each ray of the star, are single special cells (Fig. 21, *E*). In the Hymenophylleæ[3] are found pluricellular forked- and stellate-hairs. As

[1] A. de Jussieu, Monographie des Malpighiacées, p. 96, pl. II.

[2] Compare Flückiger, Pharmakognosie des Pflanzenreichs, p. 142.

[3] Mettenius, Die Hymenophyllaceen, p. 65.

examples of the latter may be named the *small* hairs of Verbascum [1], the thin-stalked stars of Lavendula Stoechas, &c. Also the short stalked, two- to many-armed hairs of Utricularia [2] and Aldrovanda [3], in which each arm is a blunt cylindrical cell, belong partly to this category, partly to the tufted hairs to be named below.

Hairs not forked, but monopodially branched, are (if we disregard cases like that described in Loasa) always pluricellular. Thus those with scattered, and sometimes repeatedly branched arms in Nicandra physaloides (Meyen, Weiss, *l. c.*), Lavendula elegans, Rosmarinus officinalis (leaf), on the inner surface of the bud-scales of Platanus (Hanstein, *l. c.*), those with whorls of branches on the leaves of Lavendula vera, species of Verbascum (e. g. V. phlomoides, the larger hairs). Also those demonstrated by Schleiden [4], which cover the leaf of Alternanthera spinosa, belong to this group. Not only is the lower part, which is attached to the foot, composed of 4–5 disk-shaped cells, one above another, but also the upper richly branched part is composed of as many cells as it bears whorls of main branches. The cells are separated from one another by transverse walls folded in deep waves, and each bulges out immediately above the transverse wall, which limits it below, into a whorl of pointed branches, and here and there, on the rest of the lateral wall, into a single branch. The form often cultivated as Alternanthera amœna shows the same structure in its scattered hairs, but with only weak development of the branchlets.

The bodies described by Weiss (*l. c.*, Fig. 76) as branchlets on old hairs of Verbesina gigantea, I was unable to find either in this plant, or in a member of the same genus, and cannot make anything of them.

Under the name of *tufted hairs*, already often used, Weiss has judiciously separated a form allied to those under consideration from the forms usually included in the term 'stellate hairs.' It arises by the division of an initial cell of a hair by a number of successive walls perpendicular to the epidermal surface, and each of the cells thus produced grows like a simple conical hair, the body of which diverges from the others, while the basal parts remain firmly united. The history of their origin justifies the position of these bodies here, side by side, with the branched, pluricellular hairs, though, as far as the mature state is concerned, one might just as well speak of a tuft of diverging simple hairs. The tufted hairs are either seated in the epidermal layer, or are borne by a thin stalk-like emergence (e. g. felty species of Solanum, as S. marginatum, verbascifolium, species of Correa), or on the apex of a multiseriate shag-hair (therefore a transitional form); this is the case in many Melastomeæ (Tetrazygia elæagnoides [5], discolor, angustifolia). Further examples are furnished by very many (all ?) Malvaceæ [6] Cistineæ; among the Labiatæ, Marrubium; species of Croton, e. g. Cr. tomentosus, J. Müll; species of Quercus, Platanus (comp. Weiss, Rauter, *l. c.*). The single rays of a tuft are usually unicellular, in Marrubium pluricellular.

2. *Capitate hairs:* erect hairs of various forms, whose free end is swollen to form a round or disk-shaped head, the transverse section of which usually exceeds that of the stalk. The head may be part of a cell, or of a unicellular hair (Fig. 21, *B*, *d*, glandular hair of Aspidium molle); or it may be itself a single cell (Fig. 31–34), or be 2– to multicellular, with the cells arranged in the most various ways in one or several layers one above another. Capitate hairs are in the large majority of cases simple. Branched ones are only known where certain branch-endings of ramifying conical hairs bear a head (hairs of the bud of Platanus [7]). The stalk bearing the head may be reduced to a minimum, to the form of a very small disk—e. g. the glandular hairs of many Labiatæ (Pogostemon, Plectranthus, Molucella, &c.; Fig. 21, *A*, *b*, *c*, 38).

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[1] Weiss, *l. c.* fig. 184.
[2] Meyen, *l. c.*; Benjamin, Botan. Zeitg. 1848, p. 58; Schacht, Beiträge, p. 28.
[3] Caspary, Botan. Zeitg. 1859, p. 128, Taf. IV.
[4] Grundz. I. 3 Aufl. p. 280.
[5] Rudolphi, Anatomie, p. 113.
[6] Compare Sachs, 2nd Eng. Ed. pp. 43, 101.
[7] Hanstein, *l. c.* fig. 96.

Capitate hairs occur on most leaf-forming plants, especially Dicotyledons and Ferns, as a rule in company with non-glandular hairs. It is true they are absent from many large groups; e. g. (all?) Gramineæ, Cyperaceæ, Palms, most Cruciferæ. To this category belong in the first place the great majority of the universally distributed *glandular hairs*: in our consideration of these we shall have to betake ourselves to single examples (Sect. 19). Meanwhile we need only remark here, that the glandular hairs are characterised by no special form, but rather by definite properties of the cell walls; therefore the terms capitate and glandular hair are not equivalent. In the case of many capitate hairs, it is as yet uncertain whether they possess the characteristic properties of glandular hairs, since in the investigation of them no attention was paid to the fundamental point, and since their external development shows no difference from that of glandular hairs. Such cases may therefore remain unnoticed here, and only a few typical examples be cited of *non-glandular capitate hairs*. The family of the Chenopodiaceæ furnishes the longest series of these: they are short hairs with a uni- or pluricellular cylindrical basal portion, which acts as stalk, and bears a relatively large bladder-like apical cell, usually of a round shape, but often irregular. They occur scattered on the leaf of many species of Chenopodium and Atriplex (e.g. Ch. album, Quinoa, Atriplex hortensis[1]), especially while these parts are young: later the bladder-like terminal cells are easily detached, and then together form a friable 'meal.' In other Chenopodiaceæ, whose leaves have a permanently white or gray surface, these hairs are so closely packed that their terminal cells (which dry up on mature parts) touch and overlap one another, forming a continuous layer over the epidermis, which does not fall off, e. g. Obione portulacoides, Atriplex rosea, A. nummularia. Hort.

Non-glandular capitate hairs occur elsewhere, e. g. on the leaf of the Pelargoniums. The petiole of Pelargonium zonale shows side by side five sorts of hair; two are sharply conical (comp. above, p. 61), the one more delicate, without septa, the other stronger and with one septum; besides these there are three sorts of capitate hairs, (*a*) glandular with short, usually 2–3 celled stalk, and large unicellular, globular, glandular head[2]; (*b*) short-stalked, with inclined, obliquely obovate terminal cell, perhaps also glandular; and (*c*) elongated hairs bearing on a usually three-celled stalk a large oval or pear-shaped head-cell, not glandular (comp. Weiss, *l. c.*, Fig. 367). Non-glandular capitate hairs with a short 1–2 celled stalk, and a globular head composed of two cells standing perpendicularly side by side, are very common among the Labiatæ, together with glands and conical hairs. On the whole, they seem to occur very often as inconspicuous structures.

II. **Scales.** Of the flat outgrowths of epidermis composed of one or few layers of cells, two forms may be distinguished, those which are scutiform, and those which are attached laterally.

The former consist of a short stalk or foot, standing perpendicular to the epidermal surface, and a more or less round, umbrella-like disk, attached by its middle to the stalk. This is usually so short that the disk lies almost on the epidermis. It is either wholly a hair-structure, unicellular (e. g. Oleaceæ) or pluricellular; or is formed, at its insertion, from a small emergence; or (Shepherdia and other Elæagneæ) it is wholly an emergence, i. e. the round scale is seated at its centre directly upon a short emergence. The scale itself consists of radially arranged cells or rows of cells, which arise by corresponding divisions (i. e. arranged, as regards the hair, radially and perpendicularly). The number of these varies greatly, from four (Jasminum) to very many. In scales where the number is large the arrangement is often irregular, especially at the centre, by reason of tangential divisions, which appear in addition to the radial ones. At the periphery the cells usually grow out radially like hairs, so that delicate stellate shapes are produced.

It is obvious from what has been said that the more simple forms of this category can hardly be distinguished from stellate hairs, such as those of Polypodium lingua (Fig. 21,

[1] Meyen, Secretionsorgane, Taf. II. fig. 1; Weiss, *l. c.* p. 559, fig. 198.

[2] Hanstein, *l. c.* p. 745.

E), Platycerium, and from capitate hairs. The families Oleaceæ and Jasmineæ[1] yield an especially complete series of forms, from the 8-celled shield, produced by triple radial division of the initial cell (Syringa), or a 16-celled shield (Fraxinus), to the 30–32-celled star (Olea Europæa). Further examples of the forms of this category are the above-named Elæagneæ, single species of Solanum (S. argenteum, Dun., and allied 'lepidota'), Croton (Cr. pseudo-china, nitens), Capparis Breynia, Andromeda calyculata, Myrica cerifera[2]. Further the leaves and stem of Callitriche and Hippuris[3], and the long-stalked scales on the leaf of Pinguicula[4]. Large scutiform scales with pluriseriate, multicellular central part, and radial multicellular margin, cover the leaf of most Bromeliaceæ, e. g. Hechtia planifolia, stenopetala, Tillandsia usneoides[5], Pholidophyllum zonatum, Billbergia clavata, Bromelia bracteata; the young leaves of many Palms, e. g. Klopstockia cerifera[6], with scales several layers of cells thick in the middle.

As regards their external development, there further belong to this category the circular, shield-shaped, glandular scales of many plants, consisting of few cells (e. g. Thymus, Salvia), or of many arranged in several series (Rhododendron ferrugineum, Humulus lupulus, Ribes nigrum, &c.). The peculiarities of their structure will be treated of later (Sect. 19).

Of scales attached at one side the Ferns yield the richest and best known examples, in their so-called chaff-scales, or Paleæ. Among these occur various intermediate forms between purely single-layered hairs, such as are many-layered at their insertion, uni- and multiseriate hairs, and shag-hairs. Their relations of size, form, and structure, so often made use of for descriptive purposes, may with a reference to the descriptive literature be here left untouched[7]. Those large branched scales on the stem of Hemitelia capensis, the similarity of which to leaves of the Hymenophyllums caused them to be described as a species of Hymenophyllum, are not to be included under epidermal structures, since they have vascular bundles, and an epidermis with stomata[8]. Uhlworm mentions in the case of Alsophila aspera thorn-emergences, which bear on their apex a large scale.

In the Phanerogams examples of this category may be sought among those forms which form shag-hairs, inasmuch as these bodies are often developed chiefly in the direction of one transverse diameter, i.e. into many-layered elongated scales. This is the case on the leaf-endings and margins of species of Papaver, in the Melastomeæ, as species of Lasiandra, Melastoma malabathricum[9], &c. To this category belong also the dermal scales, borne on scale-like emergences, of Begonia manicata and its allies. As a special very simple form allied to stellate, tufted, or capitate hairs, may finally be mentioned the scales occurring in the axils of the leaves of Hippuris and Callitriche (Hegelmaier, *l. c.*, Rauter, *l. c.*). These are borne on a short simple stalk-cell, and appear as a circular fan one layer of cells thick, which is composed of radially arranged elongated cells, or (Pseudo-callitriche) of rows of cells similarly arranged.

III. On **Shag-hairs** (Zotten) (Fig. 21, *C*, *a*, *c*) little need here be added to what

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[1] Prillieux, De la structure des poils des Oléacées et des Jasminées, Ann. Sci. Nat. 4 Sér. V. p. 1, pl. 2–3.

[2] Rudolphi, *l. c.* p. 114, where generally are very numerous details, though there is occasionally a confusion with tufted hairs.

[3] Hegelmaier, Monogr. d. Gatt. Callitriche, p. 11; Rauter, *l. c.* p. 6.

[4] Schacht, Pflanzenzelle, Taf. VII. p. 16.—Lehrbuch, I. p. 280.—Grönland, Ann. Sci. Nat. 4 Sér. III. p. 297, Taf. X.

[5] Compare Schacht, Lehrb. I. Taf. IV. pp. 10, 11; Pflanzenzelle, Taf. VII. pp. 17, 18.

[6] How far the scaly or fibrous covering of the unfolding palm leaves consists of hair structures, or of effete drying masses of tissue, requires more complete investigation in special cases. Compare Mohl, Verm. Schr. p. 177, Structura palmarum, § 82.

[7] On their development, compare Hofmeister, Vergl. Unters. p. 85.

[8] Compare Mettenius, Filices horti Lipsiensis, p. 111.

[9] Rudolphi, *l. c.* p. 115.

has been already said. The shape of their body repeats that of all single hair-forms, from which it differs only by its articulation—being pluri- or multiseriate. It terminates in a head, or is simply conical, or resembles a tufted hair; the latter for instance in the shaggy hairs of the leaves of Leontodon hastilis and incanus, which fork at their ends into 2–5 stiff conical hairs, in the shaggy hairs of the above-cited species of Solanum, Croton, and Correa (p. 62), and the Melastomeæ, where they end in a rich tuft of hairs; to these may be added Osbeckia canescens, and Medinilla farinosa. Its lateral margin is smooth, or toothed and zigzagged by the outgrowth of conically elongated cells; e. g. the conical shaggy hairs of the Hieracia, species of Papaver, and Mimosa; or it even bears tufts of hair (Correa speciosa). In shaggy hairs the foot is very often seated on an emergence. Compare e. g. the capitate glandular shaggy hairs of the leaves of Ribes (Hanstein, Rauter, Martinet, *l. c.*). The family of the Melastomaceæ has unusually numerous forms of shaggy hairs with the most various transitions to scales and tufted hairs.

IV. In the simplest case **Bladders** differ from unicellular hairs only in form, and might be called by the same name, were it not too contradictory to the original meaning of the word to call a spherical body a hair. Such unicellular round bladders, with a broad foot penetrating far below the epidermis, or borne by an emergence, are known on the foliage-leaf of Mesembryanthemum crystallinum, Tetragonia expansa and echinata, and Oxalis carnosa[1]. On the whole leaf-surface of Rochea falcata[2] and longifolia cylindrical tough bladders rounded at the top arise between the small epidermal cells; they are provided, above their broad foot, with several blunt outgrowths, which almost touch the epidermal surface. They are all of the same height, and are in close juxtaposition, so as to form an almost complete covering of the epidermis. In R. coccinea the margin alone is fringed by a single row of such bladders, which are rather elongated to the form of a short thick hair.

The herbaceous stem, petiole, and under surface of the leaf of many Piperaceæ—Piper nigrum Hort, Enkea glaucescens, Artanthe elongata—are often but not always covered in the young but almost fully unfolded state by scattered spherical bladders, as large as a pin's head, which shine like transparent pearls. These prove to be unicellular hair-structures, with a very small foot inserted in the epidermal surface, or projecting further inwards. On older parts they burst, and dry up to inconspicuous black-brown specks. Besides these there occur in the same epidermis very numerous hair-cells, which only differ from the large bladders by their small foot-cell protruding above the outer surface as an inconspicuous papilla: it may therefore be said that many hairs remain inconspicuously small, while the minority swell to form the transparent bladders.

Just the same appearance for the naked eye, with the same transitory nature, is seen in the round or oval bladders, as large as a millet seed, which Meyen[3] discovered in Begonia plantanifolia, vitifolia, Cecropia palmata, peltata, Pourouma guianensis, Urtica macrostachys, in all cases distributed as above in Piper: further in Bauhinia anatomica, especially on the stem when several years old. These he named pearl-glands. Such structures are often observed also on Vitis, Ampelopsis[4] (A. quinquefolia, Veitschii), Cissus velutina, also on Pleroma macrantha (Melastomaceæ). These pearl-bladders (those of Pleroma have not been investigated) coincide with those mentioned for Piper in this point, that they are chiefly composed of very large bladder-like cells, which are thin-walled, and contain, besides radially-striated protoplasm, much watery fluid, and a number of brilliant colourless globules of resin or oil. In other points their structure differs. In the Begonias, according to Meyen, they are hair-structures which are allied to capitate shaggy hairs. The body of the pearl consists of about a dozen cells of the above

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[1] Meyen, Secretionsorg. Tab. VII. figs. 8–16, 38, 39.—Weiss, *l. c.*

[2] K. Sprengel, Anleit. z. Kennt. d. Gew. 2 Aufl. I. p. 113, Taf. III.—A. Brongniart, Ann. Sci. Nat. 1 Sér. XXI. p. 453, Taf. 10.

[3] Secretionsorgane, p. 45, Taf. VII.

[4] Hofmeister, Handb. Bd. I. p. 545.

character, arranged in two irregular rows, and is borne by a bi-seriate shaggy hair, as stalk. As in Piper there are also found small club-shaped shaggy hairs, from the swelling of which the pearls might have been derived.

The pearls of the above-named Ampelideæ are, on the other hand, emergences. They consist of several large cells of the character above-stated, and are covered by a protrusion of the epidermis consisting of numerous relatively small hyaline cells. On or near the summit of the body is a stoma, which is widely open, and on old specimens is further extended by rupture at the corners of the slit. Young specimens are seated on the surface as blunt warts, with broad base. In old specimens the upper part swells so much that the point of insertion appears as a relatively small stalk. The pearls of Urtica macrophylla, and, according to Meyen's statement, of the other Urticaceæ, have in the main a like structure, with the difference that they are without the stoma. The pearls of Cecropia and Bauhinia are, according to Meyen, similarly composed; they are also without the stoma, and differ further in their tissue consisting throughout of small very numerous cells.

V. **Prickles** and **Warts**. It was above stated that the massive outgrowths termed prickles and warts are mostly emergences, in the formation of which epidermis and subepidermal tissue conjointly take part. For the majority of these structures, as the prickles of species of Dipsacus, Rosa, Gunnera, Smilax, Solanum, and Ribes, the Cactaceæ, &c., this is thoroughly proved by late investigations of the history of their development (Rauter, Kauffmann, Warming, Delbrouck, Uhlworm). Delbrouck and Uhlworm, however, have both shown that exceptions to the predominant law exist, since the prickles of the investigated species of Rubus (R. cæsius, idæus, Hofmeisteri) and those of the petiole of Chamærops humilis belong to the epidermis, and differ only in form and consistence from shaggy hairs. Further that the warts on the foliage leaf and carpels of Bunias Erucago are at least chiefly derived from the epidermis. If once an anatomical distinction is adopted, it is necessary to separate the above outgrowths of epidermis from emergences of the same or similar form, however closely they may correspond to them—and to many sorts of hair-formations of most simple structure—as regards their physiological or teleological significance.

The often-described oval warts of Dictamnus[1], which bear on their apex a short, septate hair, are connected with the above forms. They will be described more in detail below (p. 69).

2. STRUCTURE OF THE ELEMENTS OF THE EPIDERMIS.

(a) *Protoplasm and Cell-Contents.*

Sect. 11. The wall of the **Epidermal cells** both in one-layered and many-layered epidermis encloses as a rule a delicate protoplasmic sac with distinct nucleus, and within this clear transparent cell-sap, which is either colourless, or tinted with dissolved pigments (Erythrophyll, &c.). It is to this condition (and the colourless membrane) that most epidermal layers owe their great transparency.

In the majority of cases chlorophyll and starch are absent from epidermal cells[2]. This is the case without exception in land plants where the tissue is very thick-walled, and surrounded by air; often also in thin-walled cells occurring under similar conditions. But in not a few other land plants more or less numerous chlorophyll grains, eventually with included starch, lie in the peripheral protoplasm.

[1] Meyen's (Secretionsorg.) 'Mützenförmige Drüsen.' Compare Hofmeister, Pflanzenzelle, p. 259; Rauter, *l. c.* Taf. V, VI.

[2] [Cf. Stöhr, Bot. Ztg. 1879, p. 581.]

If one surveys the cases in which this occurs, it will be seen that the foliage of plants with delicate leaves, which live in shady places, is especially concerned, such as that of most Ferns, further Impatiens nolitangere, Melampyrum sylvaticum, Galeopsis tetrahit, Ranunculus Ficaria, Epilobium roseum; also Listera ovata, and Staphylea pinnata [1] may perhaps be added. On the other hand, however, the same phenomenon occurs also in inhabitants of sunny places, as Mercurialis annua, Lamium purpureum, Caltha palustris, to which examples many others might easily be added. Epidermal cells of parts growing under water are, on the contrary, rich in chlorophyll grains and the bodies included in them, richer even than any other tissue of the species. Thus in the leaves of Ceratophyllum, Aldrovanda, Ranunculus aquatilis, Potamogeton, Hydrilleæ [2], &c. In Elodea canadensis, and its allies, the chlorophyll-containing leaf consists in the main of only two layers, which originate, like scales, from the epidermis of the stem. Brongniart [3] already showed that in species typically submerged, but which also occur as land plants, such as Ranunculus aquatilis, the submerged epidermis is rich in chlorophyll, while that of the land form is without it, and that an intermediate condition occurs on transition from one habit to the other. But the rule just given is not general for all water plants. Both the amphibious species of Callitriches and C. autumnalis which only occurs submerged, have an epidermis without chlorophyll [4].

Sect. 12. In contrast with the epidermal cells, the *guard-cells of the stomata* are always very rich in protoplasm, chlorophyll, and the bodies included in the latter, especially starch grains; in colourless plants only the last-named bodies are present. The subsidiary cells of the stoma resemble the epidermal cells as regards the properties in question. No peculiar phenomena, i.e. such as do not belong generally to the different cells of the plant, are known for the cell-sap of the epidermal and guard-cells, and the bodies which occur dissolved and suspended in it. It is true they have as yet hardly ever been carefully investigated. This assertion is only confirmed by the casual statements made about oily drops suspended in cell-sap, and masses or drops containing tannin in the Cycadeæ (Kraus), about tannin generally in the Crassulaceæ, Rosa, Ficus, Camellia, the Saxifragas [5], &c.: also about more or less solitary crystals of Calcium oxalate in the leaves of Tradescantia discolor, Begonia manicata, argyrostigma, and Hakea saligna, octohedral crystals in Asplenium Nidus, klinorhombic crystals which completely fill the small cavity in scattered or grouped cells of the leaf of Ilex paraguayensis [6].

Thomas [7] describes in the leaves of Pinus Pumilio, Pinaster, and austriaca, epidermal cells whose contents are dried up, and replaced by air in consequence of rupture of the membrane. It may, however, be conjectured that this description refers to abnormal conditions.

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[1] Sanio, Botan. Zeitg. 1864, p. 196. Compare also Kraus, in Pringsheim's Jahrb p. 314.

[2] Caspary, Pringsheim's Jahrb. I. p. 348.—Botan. Zeitg. 1859, p. 125.

[3] Ann. Sci. Nat. 1 Sér. tom. XXI. (1830) pl. 17, figs. 3 and 6.—Further, Askenasy, Botan. Zeitg. 1870, *l.c.*

[4] Hegelmaier, Monogr. p. 9.

[5] Compare Sanio, *l.c.*; Kraus, *l.c.*; Wigand, Botan. Zeitg. 1862, p. 121; Engler, Botan. Zeitg. 1871, p. 888.

[6] Kraus, *l.c.*—Meyen, Physiologie, I. p. 227.—Goldmann, Botan. Zeitg. 1848, p. 557.

[7] Pringsheim's Jahrb. p. 26.

Sect. 13. The cells of **Hair-structures** are, while young, provided like other young cells with a well-developed protoplasmic body, and many while in this condition quickly attain a great size, so that they are specially suitable and easily obtained objects for the study of the protoplasmic body. Mature hairs behave in two different ways as regards their protoplasmic body and their contents. Those of the first category resemble, in short, the epidermal cells, having a permanent protoplasmic body, usually in the form of a delicate sac-like lining to the cell-wall; more rarely the protoplasm persists for a longer time in considerable quantity (stinging hairs of Urtica, Hairs of Cucurbita, &c.). The cavities in the protoplasm are permanently filled with watery cell-sap (*Sap-containing Hairs*). In hairs of the second category the protoplasm and cell-sap dry up when growth stops, and are replaced by air. These persist as *air-containing* hair-structures. The capitate hairs *containing mucilage* in Osmunda regalis are hitherto unique, and will be described below (Sect. 19).

All root-hairs and a large number of the hair-structures which occur on foliage leaves contain cell-sap. They can be distinguished at once from those of the other category by their transparency. Their protoplasmic body and contents show the same series of various modifications of special character as is the case in the epidermal cells. Most of them, e.g. all root hairs, all (?) stinging hairs, &c., are devoid of chlorophyll. Others have more or less abundant grains of chlorophyll and allied pigments. The correspondence with the epidermal cells extends also, as far as is known, to the substances mixed with the cell-sap (comp. Weiss, *l. c.* 645).

The contents of the often-described stinging hairs have special peculiarities, which are also said to occur in many hair-structures described as glandular hairs of various categories.

We know of the erect stinging hairs of the Urticaceæ, Loaseæ, and other plants named above (page 60), which resemble one another so remarkably in structure and form, that the brittle point (Sect. 22) breaks off when touched, and that a fluid issues through the hole thus made, which causes more or less slight inflammation when applied to the human skin, especially if it enters the small wounds caused by touching the hair itself. It is further known of this fluid that it has, like most cell-fluids, an acid reaction, not alkaline as stated formerly [1]. On the fact that by distilling the nettle plant with sulphuric acid formic acid is obtained, the conjecture has been founded that the latter substance causes the phenomena of stinging [2]. But as a matter of fact nothing is known of the active substance, not even whether it is to be sought for in the acid fluid, or in the protoplasm [3].

The apical cells of capitate hairs are often distinguished by very dense protoplasmic contents, in which resinous substances may be shown to be present. Hanstein (Bot. Ztg. *l. c.* p. 748) states that in the multicellular capitate hairs of Salvia all the cells may finally be united by the solution of their membranes into one fluid mass (containing Resin or Balsam) which is surrounded by the bladder-like cuticle. In the

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[1] P. de Candolle, Physiologie, übers. v. Röper, I. p. 193.

[2] Von Gorup-Besanez, in Journ. f. pract. Chemie, XLVIII. p. 191.

[3] Compare the neat paper of Duval-Jouve (which however gives no new information), 'Sur les stimules d'ortie,' in the Bulletin Soc. Bot. France, XIV. p. 36.

often described club- or egg-shaped warts of Dictamnus, which end in a short hair, there are found cell-contents of a character exceptional for epidermal structures. The cells finally fuse to form intercellular balsam-containing cavities[1]. These, as Rauter has carefully shown, are multicellular bodies derived from a single epidermal cell, consisting of a permanent peripheral layer of epidermal cells with scanty contents, running out into the terminal hair, and an inner multicellular mass. The cells of the latter contain, about the end of their growth, at first chlorophyll; then there appear drops of resin and ethereal oil in increasing quantity; these finally unite to large drops, which fill the cavity formed by the solution of the inner cell-walls (comp. Fig. 22). Beneath the epidermis, but derived in part from it, there arise in Dictamnus similar cavities containing ethereal oil. Martinet (*l. c.* page 176) describes in Cuphea lanceolata long, multiseriate, shaggy hairs consisting of elongated cells: in the broad base of each of these is enclosed a central round body consisting of many small isodiametric cells. This resembles the central tissue of the warts of Dictamnus in its position and its contents, which apparently include drops consisting of ethereal oil: but the solution of the cell-walls, which occurs in the latter case, was not observed in the former. Peculiarly formed groups of cells, characterised by their dense contents, which turn brown on drying or treating with alkalies, and which protrude little or not at all above the outer surface, and only slightly inwards, occur in numbers in the epidermis of the tubular leaf of Sarracenia[2]. They are globular, or flask-shaped, with the neck directed outwards, and consist of about 16 small cells derived apparently from the division of one epidermal cell. Their structure has been well described by Vogl from dried material. Their origin and signification remains still to be investigated.

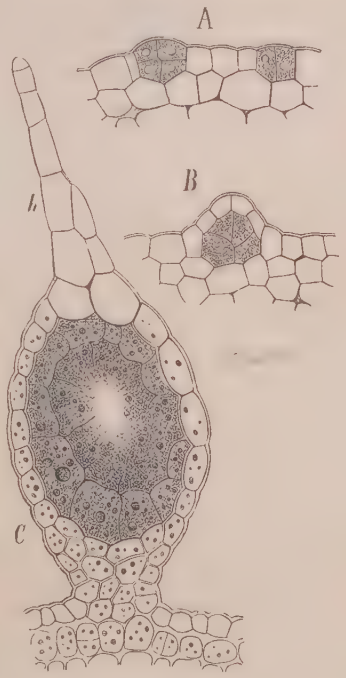

FIG. 22.—Dictamnus fraxinella; oil-containing dermal warts, cut perpendicular to the surface. *A* youngest stage of development; *B* rather older; *C* (220) median section through a mature specimen. After Rauter, from Sachs' Textbook.

Those cells and cell-groups belonging to the epidermis, which have contents of peculiar nature, such as in the above examples, are often described as *glands* if they are also characterised by special form. This term will be discussed in Sect. 19.

Air-containing dry hairs, scales, or shaggy hairs, form dry opaque coverings which appear of different colour according to the character of the membranes and

[1] Meyen, Secretionsorg. Taf. I. pp. 28, 29.—Unger, Anat. und Physiol. p. 212.—Hofmeister, Handb. I. p. 259.—Rauter, Martinet, *l. c.*

[2] A. Vogl, Phytohistolog. Beiträge. Sitzgsber. d. Wiener Acad. Bd. 50 (1864).

of the remnants of the cell-contents, and present a lustre which varies according to their form and position and the character of their surface. They preponderate in very hairy plants. Thus the dense white felt on the foliage of many Labiatæ (Stachys, Teucrium, Salvia, &c.), Compositæ (e.g. Gnaphalium), the Verbascums, Banksias, Rubus idæus, &c.; the silvery white or brown peltate scales of the above-named Elæagneæ, Bromeliaceæ, Croton, Solaneæ, Olea spec.; the rustling 'Paleæ' of the Ferns; the white crust consisting of dried capitate hairs in the above-quoted (p. 63) species of Atriplex, and Obione, and other Chenopodiaceæ.

(b) *Structure of the walls of the Epidermal Elements.*

Sect. 14. The wall of the **epidermal cells** is, in very delicate parts, a thin cellulose membrane developed pretty equally all round. In rather more firm parts, in such as are termed herbaceous, and to a greater extent in very tough parts, such as stems and branches of smooth-barked ligneous plants, leathery and fleshy leaves, it is strongly thickened. In rare cases the thickening is almost equal all round, e.g. leaves of Ceratozamia mexicana[1], Pinus sylvestris, and its allies[2] (Figs. 11, 27; in this case the lumen almost disappears), or is much less on the outer surface than on the lateral and inner ones, as is the rule in the Bromeliaceæ (Fig. 12, p. 37)[3]. Also in the epidermal cells containing mucilage, which will be described below, the inner wall is of considerable thickness, often exceeding that of the outer wall. In an epidermis one layer thick and in the outer layer of a many-layered epidermis the outer wall is usually thicker than the lateral or inner walls. In the above-named tough parts, such as leathery and fleshy leaves, old branches of Viscum, Ilex, Laurus, Menispermum canadense, Palm stems, &c., it is often thickened to such an extent that it occupies the greater part of the whole volume of the cell. The thick outer wall is either sharply marked off from the thin lateral walls or graduates gently into them. The walls of the inner layers of a many-layered epidermis all resemble in the main the lateral and inner walls of the single-layered epidermis as regards strength and structure, with the exception of isolated peculiar cases which must be mentioned as being extraordinary.

The thickened walls have generally the well-known structure of cell-membranes, stratification, striation, and pitting, but never fibrous thickening of the walls. The phenomena connected with special peculiarities of substance — cuticularisation, formation of Cystoliths—will be treated of later. There occurs sometimes on the wavy lateral walls (e.g. under surface of the leaf of Helleborus fœtidus[4]) at the bottom of a depression a local thickening in form of an excrescence resembling a fold or doubling of the membrane, which protrudes inward, at right angles to the surface.

Pits of the usual form, corresponding on opposite sides, are very common on the lateral and inner walls. As a rule they do not occur on the thick outer walls,

[1] Kraus, Cycadeenfiedern, *l. c.*

[2] Thomas, *l. c.* p. 25.—Hildebrand, Botan. Zeitg. 1860, Taf. IV.

[3] Von Mohl, Verm. Schriften, Taf. X. 33.—Schacht, Lehrb. I. Taf. IV. fig. 10.

[4] Von Mohl, Verm. Schr. Tab. VIII. fig. 21; Vegetab. Zelle. p. 14. Compare also Cohn, Nov. Act. Acad. Leopold. vol. XXII. pars 2.

still they are present in a considerable number of exceptional cases. Thus on the foliage leaves of Coffea, Viburnum Avabaki, Cocculus laurifolius, Cinnamomum aromaticum, Camellia japonica[1], and of Grasses[2], where some of them are arranged perpendicularly to the outer surface; but on the undulating corners they are directed obliquely outwards from the lumen of each cell, and facing the neighbouring cell, so that those of two neighbouring cells cross. They occur also in Abies[3], Cycas[4], Lycopodium pinifolium[1], and Equisetum hiemale (comp. Fig. 24 *B*[5]). The walls of the elongated epidermal cells of the upper side of the leaf of Acropteris australis show a spiral striation, as the result of peculiar pitting (comp. Sect. 30). The free surface of the outer walls is often quite smooth: but is not uncommonly uneven by reason of small thickenings protruding outwards: short warts, e.g. in species of Equisetum, leaves of Sparganium ramosum, Aloe verrucosa, Radula, Crassulaceæ (comp. Fig. 20, p. 53), &c.: bands, which are relatively broad and blunt, e.g. leaf of Helleborus niger, fœtidus[6], Dianthus Caryophyllus, plumarius, or thin and sharp, as in very many leaves and petioles, e.g. Allium Cepa, Eucomis, Rumex Patientia[7], obtusifolius. The bands often run nearly straight and parallel, and are then usually longitudinal relatively to the whole body, rarely (Eucomis) they are transverse; not uncommonly they are wavy and branched (e.g. Helleborus, Pirus communis), and in the majority of cases they are continuous from one cell to the next.

The wall of the *stomatal cells*[8] is usually, but not always, thinner on the average than that of the adjoining epidermal cells. It is in most, and one may say in regular cases, unequally thickened in such a way that a strongly thickened ridge runs along the entrance and exit of the slit (Fig. 23). These ridges protrude on the free surface as the above described ridges of entrance and exit, which are sharp-edged and concave towards the slit; rarely both are almost equally strong (Lilium candidum, Ficus elastica); usually the ridge of entrance is much stronger than the other, and in superficial stomata of tough leaves it often takes the form of a high and thick wall, e.g. Clivia nobilis, many Proteaceæ, Pholidophyllum zonatum (Fig. 12, p. 37), Epidendron ciliare, Octomeria, Sarcanthus rostratus, &c. The ridge of exit is often extremely small (leaf of Pholidophyllum, Dianthus caryophyllus, Lomatia longifolia, Sparganium ramosum), or is not present at all (comp. p. 35). The thickened ridges either protrude into the cavity of the cell as flattened swellings, or not at all. The remainder of the wall of the guard-cell, that is the convex side

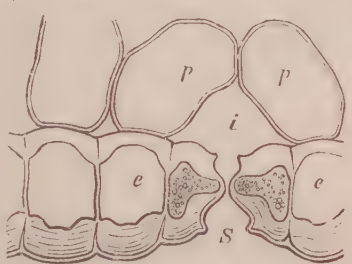

FIG. 23.—Hyacinthus orientalis; *leaf*, transverse section; *e* epidermal cells, *S* entrance of the stoma, which is cut in median transverse section; *i* the respiratory cavity, between the parenchymatous cells *p*. (800). From Sachs' Textbook.

[1] Kraus, *l.c.* p. 318.
[2] Von Mohl, Verm. Schr. Taf. IX.
[3] Thomas, Hildebrand, *l.c.*
[4] Von Mohl, *l.c.* Taf. X.
[5] Sanio, Linnæa, 29, p. 169.
[6] Von Mohl, Verm. Schr. Taf. IX. 6-8.
[7] Von Mohl, *l.c.* figs. 3–5.
[8] Compare the papers quoted above, sect. 5, especially Von Mohl, Spaltöffn. d. Proteaceen; idem, Botan. Zeitg. 1856, *l.c.*; and the large series of good representations in Strasburger's work, Pringsheim's Jahrb. V.

which is turned from the slit, the united ends, and the strip of the concave side which borders on the slit is much less thickened. The last-named strip is seen, in those cases where ridges of exit and entrance protrude far into the cavity, as a channel on the inner surface of the wall, which appears in the transverse section of the stoma like a broad pit. When the ridges of exit and entrance are very broad, the middle of the convex side assumes a similar appearance (e.g. Ficus elastica, Fig. 18 *C*). The various modifications of this plan of structure, depending upon the absolute and relative strength of the thickening and its varying protrusion inwards and outwards, require no further description in detail; some of them are evident from the above figures. Further, as regards genuine exceptions, which occur especially in the Coniferæ and Cycadeæ, we may refer to the special literature above-quoted (comp. p. 35). Still the structure of the walls of the stomata of Equisetum, which is anything but clearly explained in the writings of Duval-Jouve and Milde [1], must not be entirely passed over (Fig. 24)[2]. The guard-cells themselves are here in no way

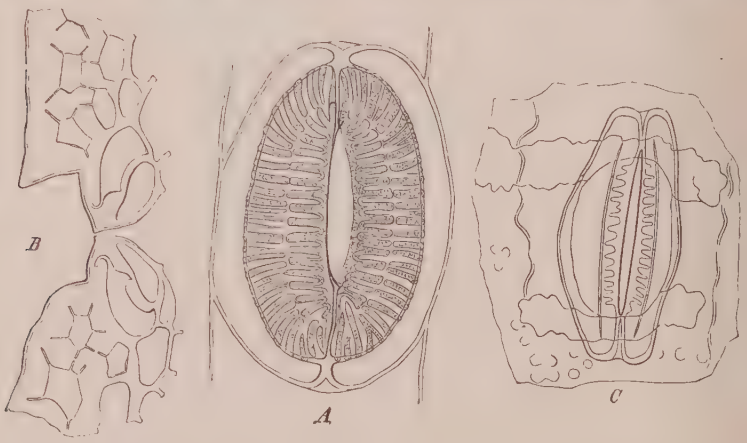

FIG. 24.—Stem of Equisetum hiemale; stoma with the surrounding tissue (390). *A* view from the inner surface. The pair of guard-cells is surrounded by the superposed edge of the pair of subsidiary cells. *B* transverse section of the stem passing in a median direction through a stoma, which lies in a depression of the surface. The narrow entry of the slit is bordered by two flat guard-cells and the subsidiary cells which surround them; each of the latter has a curved pit, turned outwards. Further explanation in the text. The cells of the single-layered epidermis and of the hypodermal schlerenchyma below it have numerous pits. *C* silica residue of a fragment of epidermis with a stoma, after maceration in Schultze's mixture and subsequent ignition; seen from outside. The curved figures are the outlines of the prominences of the outer surface.

remarkable except in their form, which is flattened obliquely outwards, and in the slight difference in thickness between the ridges of exit and entrance and the other bands of the membrane. But the subsidiary cells, which completely surround them (comp. p. 43), have a thickening on the wall bordering on the guard-cell, in form of bands protruding into the cell-cavity. These diverge in a radiating manner from the slit. Hence the beautiful radiate-marking seen in surface view. The number, breadth, and frequent branching of the radial bands vary according to species. In Milde's Equiseta phaneropora (at least E. limosum) each band runs over the whole radiate

[1] Milde, Monographia Equisetorum, Nov. Act. Acad. Leopold. tom. XXIV. pars II.—Duval-Jouve, Histoire nat. des Equisetum de France, Paris, 1865.

[2] Sanio, Linnæa, Bd. 29, p. 389, Taf. III.—Strasburger, *l. c.*

surface, the slit is therefore surrounded by a series of radiate bands. In Milde's E. cryptopora (at least E. hiemale) the striated wall is traversed about half way between the slit and the convex outer border by a narrow oblique furrow, which is almost parallel to the slit, and this divides two concentric series of radial bands, one of these next the slit, the other on the side opposite to it (Fig. 24).

What has been said of the walls of the epidermal cells holds in the main for those of hair-structures. Those walls which separate the cells of multicellular hairs resemble on the whole the lateral and inner walls of the epidermis. Their details of structure are, if possible, more various than their modifications of form. Projections of the outer surface, in form of ridges, warts, or even of those sharp prickles represented in Fig. 21 *B*, appear in hairs more commonly than in the epidermal cells. The stiffness of the hairs depends upon the thickening of the walls, which may proceed till the lumen is obliterated. A hard, rigid hair or shaggy hair, is called a bristle or seta. If it is also conical and sharp one can prick oneself with it, as with the horizontal hard bristles of Malpighia urens, or the rigid hairs of the Borragineæ and Cucurbitaceæ. In this property, so disagreeable to men, lies the ground for the often-asserted similarity of the hairs of the Malpighiacæ to the stinging hairs, and of puncturing bristles to prickles.

Sect. 15. The cell-walls of the epidermis are cellulose membranes; a number of other bodies are embedded in, or superposed on this: Cuticular-substance or *cutin*, *wax*, *resin*, *volatile oils*, *gum* and *bassorin*, compounds of *silicon*, and *lime salts*, bodies with whose presence remarkable peculiarities of structure are connected.

Sect. 16. Of the relatively pure layers of cellulose of epidermal membranes it may be said that in the majority of cases, especially in herbaceous parts, they appear similar to that watery highly refractive modification of cellulose membranes which is characteristically developed in the Collenchyma, to be described later. The detailed investigations necessary for an exact statement on this point have not been made.

Allied to these watery cellulose layers are the parts of the membrane of epidermal cells, which have been altered to *vegetable mucilage* and *bassorin*; Radlkofer[1] has lately drawn attention to the frequent occurrence of these substances in foliage leaves. The thickened inner wall of these epidermal cells consists, especially in their inner layers, in the mature condition, of a vegetable mucilage, which swells in water till its identity is lost, like the mucilage of Linseed, &c. These layers of mucilage are developed especially strongly on the leathery leaves of the Cape Diosmeæ (Diosma alba, Agathosma spec., leaves of Buku[2]), where they are found on the upper side of the leaf, which has no stomata, and in the parts of the under surface where stomata are absent. The cells in these parts are of a great height, their outer half has the usual structure of tough cuticularised epidermis. The whole of the inner half, which is often large, is filled with the stratified mass of mucilage, which is limited on the exterior by a level surface. This body swells on addition of water or glycerine to such an extent that it lifts the whole outer parts of

[1] Monogr. d. Gattung Serjania, p. 100 (1875).

[2] Compare Flückiger, Schweizerische Wochenschrift f. Pharmacie, Dec. 1873.

the epidermis far from the inner tissues of the leaf, and appears itself like a special mucilaginous layer of tissue.

The same phenomenon, but apparently always developed to a less extent, was found by Radlkofer in the foliage leaves of numerous Dicotyledons; e.g. Sapindaceæ, species of Salix, Daphne, Quercus pedunculata, Betula alba, Erica carnea and Tetralix, species of Prunus, Genista, Cytisus spec., &c., of Ferns in Botrychium Lunaria. As shown by Radlkofer's comparative review of the cases investigated, the phenomenon is by no means generally distributed, nor is it generally peculiar to definite forms of leaf or systematic groups; it is absent, e.g. in Salix alba, amygdalina, Betula fruticosa, Prunus Padus, &c. In the Sapindaceæ investigated by Radlkofer it is often only single cells, or groups of cells, which show the phenomenon in question.

Cutin occurs in form of the *cuticle*, and in the *cuticular layers* of the cellulose membrane[1].

Cutin is a non-nitrogenous carbon compound, which is completely combustible; it is dissolved, or destroyed by boiling solution of potash, and by Schultze's mixture; it can therefore be completely removed from the epidermis by these reagents. It is only slightly attacked by mineral acids, especially sulphuric acid, which destroy cellulose. It remains unaltered in ammoniacal sub-oxide of copper after previous treatment with acids; the same is the case with water, alcohol, and ether. It resists rotting far longer than cellulose. By these reactions the means are supplied for isolating the cuticle and the cuticular layers. Iodine preparations, with or without the assistance of sulphuric acid, colour the cuticle and cuticular layers yellow or brown. Aniline dyes are quickly taken up by them in large quantity, and deep coloration is the result. From a mixture of aniline red and violet, the latter is often (not always) taken up more abundantly[2].

The *cuticle* covers the whole outer surface of the epidermis, including the hairs, as a thin, always closely applied hyaline skin. It appears, *secreted on the outer surface of the cellulose walls*, on the embryo while it consists of only few cells, and covers it henceforward as well as the *punctum vegetationis* of the stem and all the members which appear on it, always following the growth of these by means of corresponding surface-growth, while its increase in thickness is infinitely less. This continues till the epidermis is eventually thrown off. In rare cases, when the original epidermis is destroyed early, and is then replaced by new elements (the leaves of the Aroideæ mentioned on p. 29, and perhaps also of Palms), there appears also over the latter a new cuticle. It is wanting at the *punctum vegetationis* of the root, but appears behind it, where the differentiation of the epidermis begins. The cuticle is continuous over the surface of the guard-cells, through the stoma, into the respiratory cavity, from the moment when the formation of the slit begins by separation of the two cellulose lamellæ. It usually continues over the walls of the respiratory cavity as far as these are formed from the epidermal cells. It becomes gradually thinner as it proceeds inwards, till it ceases where the respiratory cavity is laterally bounded by subepidermal cells. It thus forms at each stoma an open tube which passes

[1] [Cf. Von Höhnel, über die Cuticula.—*Ref.* Bot. Jahresbericht, 1878, I. p. 16.]
[2] Hanstein, Botan. Zeitg. 1868.

from the slit inwards. In the Cacteæ, it extends from the slit onwards over the whole wall of the spacious respiratory cavity, and sends tubular branches with open ends into the intercellular spaces of the neighbouring chlorophyll-containing parenchyma[1]. It is wanting as a rule on the inner surface of the epidermis. It is rarely continued from the slits onwards over the whole inner surface of the epidermis, as far as this borders on intercellular spaces, as a lamella, which is interrupted by the surfaces of insertion of the subepidermal cells (v. Mohl, *l. c.*). This is the case on both the stomata-bearing surfaces of the leaf of species of Armeria, especially A. plantaginea, on the under surface of the leaf of Betula alba, Dianthus caryophyllus, Euphorbia Caput-Medusæ, and the stomata-bearing bands of the leaf of Asphodelus luteus. In Helleborus niger and viridis the inner cuticle extends from the stomata-bearing under surface, over the upper side of the leaf, which has no stomata. (On the occurrence of cuticle in the deeper-seated intercellular spaces, comp. Chap. VII ; on the peculiar phenomena in Restio diffusus, see Sect. 18.)

In the well-established cases, the cuticle cannot by the means of investigation at present in use be separated either mechanically, or optically, into separate parts or segments corresponding to the neighbouring cells. By careful maceration with potash or dilute acids, it may be separated as a continuous skin from large tracts of the underlying cell-membranes. It appears by the action of the above reagents to swell more strongly in the direction of the surface than those membranes. By boiling solution of potash, or Schultze's mixture, it is transformed into a tough shiny mass, and then completely destroyed without leaving a cellulose residue. It is in most cases very thin, especially on submerged parts and roots ; on aerial parts, not excepting the *punctum vegetationis*, it is thicker ; only in few cases where it is specially strongly developed (leaf of Cycas revoluta, Ilex aquifolium), a delicate stratification can be recognised ; as a rule, there is no sign of this. Its thickness is usually equal all over one and the same surface ; also on the ridges and warts of the surface so often mentioned the cuticle itself usually runs unthickened over the corresponding outgrowths of the wall (e. g. leaf of Eucomis, Orchis, Helleborus, &c. Comp. also v. Mohl, Verm. Schr. Taf. IX. Figs. 7, 8). Projecting thickenings belonging to the cuticle itself are much more rare ; on the hairs of Monotropa Hypopitys[2] there is the most exquisite example of this ; the outermost layer of the wall, which is covered with numerous elongated warts, here shows the properties of the cuticle : it is completely dissolved in boiling potash, and leaves the cellulose membrane quite smooth.

On some very thick epidermal layers, which form large quantities of wax (Acer striatum, Negundo, Sophora japonica), the cuticle follows the increase of thickness of the membranes only a short time, and then breaks up by irregular splits.

Where the epidermis is delicate the cuticle covers the relatively pure cellulose membrane of the epidermal cells. But where it is thicker, especially when long-lived, the part of the cellulose membrane bordering on the cuticle itself also contains cutin, and consists of layers of cellulose, each of which is permeated by cutin.

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[1] Von Mohl, Botan. Zeitg. 1845, p. 3.—Unger, Grundzüge (1845), p. 25.

[2] Schacht, Lehrbuch, I. p. 140.

According as this is the case, the membrane shows the characteristic reactions of cuticle. Treatment with the reagents, which dissolve cutin, removes it successively from the persistent cellulose membranes, which retain their original form and structure, though necessarily with considerable loss of substance (comp. Fig. 25). These layers containing cutin are called *cuticularised*, or *cuticular layers*[1].

The cuticularisation may extend over all the elements of the epidermis, including the epidermal cells, the hair-structures, and the cells of the stomata also. On the latter the cuticular layers are it is true often thinner, in correspondence with the smaller size of the cells, but often, especially in the ridges of entry, they are strongly developed, and are continuous with those of the neighbouring cells, e. g. leaves of Clivia nobilis[2], Dasylirion[3], Epidendron ciliare and other tough-leaved Orchideæ, Ficus elastica, &c.

The cuticularisation is evenly continuous over the epidermal cells of one surface, and in the above-mentioned cases over the stomatal cells also, so that one cell resembles another: thus the cuticular layers, in a simple case, appear in a transverse section as an even broad band surrounding the whole epidermis. The cells of the epidermis may be separated from the cuticle, which covers them, both optically and (by help of the above-named reagents) mechanically. The latter fact is certain, though it is not always easily done. The form, relative thickness, and extension of the cuticle over the cell-walls connected with it is no less various and characteristic in special cases than the other relations of form and structure above described. The following typical forms may accordingly be distinguished:—

1. The cuticular layers form in the great majority of cases a covering on the outer side of the epidermal cells, which is sharply marked off internally from the non-cuticularised membrane. This may be—

(*a*) A layer of almost universally equal thickness, which follows the surface, and does not attain a thickness equal to that of the outer wall; e. g. leaf of Dianthus plumarius, Caryophyllus, Helleborus fœtidus, Vanilla, Galanthus nivalis[4], &c.

Or (*b*) a thick layer, which follows the outer surface, and projects inwards in the shape of a ridge, of a conical form, in the middle of each lateral wall, and where several cells join. The projections are usually sharply wedge-shaped towards the inside, and do not reach as far as the inner wall (Fig. 25). Or they reach as far as the latter, and are continued into the layer ('intercellular substance') which marks the limit towards the subepidermal layer, and which is also cuticularised; e. g. branches of Jasminum officinale, Ephedra distachya, leaf of Phormium tenax[5], Ilex (Fig. 26), and Pinus (Fig. 27).

The non-cuticularised layer (coloured blue with Schultze's solution), which in all these cases surrounds the cell-cavity, is either relatively thick, and consists of many layers, as in the leaves of Pinus, Ilex (leaf-nerves), many species of Aloe,

[1] Von Mohl, Botan. Zeitg. 1847, p. 502.
[2] Von Mohl, Botan. Zeitg. 1856, *l. c.*
[3] Schacht, Lehrbuch, I. Taf. IV. fig. 9.
[4] Von Mohl, Verm. Schriften, p. 260 ff.—Wigand, Intercellularsubstanz u. Cuticula (1850), fig. 96, &c.—Petunikow, Recherches sur la Cuticula, p. 191, figs. 1, 22 (Bulletin Soc. Imp. de Moscou, 1866).
[5] Von Mohl, Verm. Schriften, Taf. X. fig. 28, 27.

Agave americana, Epidendron ciliare, Dasylirion, Sanseviera zeylanica, and the phylloclades of Ruscus aculeatus; or, in so far as it borders on the cuticular layers, it is a very thin layer, which in many cases can only be observed with certainty in very good preparations. This is most frequently the case where the epidermis is thick. Examples: leaf of Hakea ceratophylla and other species, Ilex aquifolium (surface of leaf), Hoya carnosa, Taxus baccata (under surface of leaf); one-year-old branches of Viscum album [2], Taxus, Rosa canina, Kerria japonica, Ilex aquifolium, Jasminum officinale, Laurus nobilis, Sassafras, Acer striatum [3], &c.

(*c*) The whole outer wall is cuticularised, the rest of the wall not. The upper side of one-year-old leaves of Taxus baccata, one-year-old stems of Salix daphnoides, and, according to v. Mohl (Verm. Schr. Tab. IX. 15), epidermis of the stem of Kleinia neriifolia.

2. The cuticular layers and the non-cuticularised part of the wall are not sharply defined one from the other, but rather—

(*a*) either the inmost lamella of each cell-wall is not cuticularised, while the outer layers show the cuticular reaction gradually stronger the further they are from the inmost layer; e. g. stem of Psilotum triquetrum, young stems of Selaginella inæqualifolia, Martensii, &c.;

(*b*) or the whole wall of the epidermal cells is cuticularised all round: petiole of Arbutus Unedo [4], two-year-old branches of Nerium oleander [5], leaf of Elymus arenarius [6], stem of Klopstockia cerifera [7], leaf of Pinus, Abies, Cunninghamia lanceolata, older stems of the above-named Selaginellas. Further, the brown-walled epidermis of the stems and petioles of very many Ferns belongs to this category.

3. The epidermis of the pinnæ of the leaf of Cycas revoluta may be cited as an exceptional case [8]. The pitted cellulose walls of the epidermis are covered externally by a thick cuticle, which is stratified, but not separable into cuticular layers. From the cuticle there run narrow limiting bands of cuticular substance between the lateral walls of the cells, to the subepidermal tissue.

Where the cuticular layers border on non-cuticularised membrane the limiting surface is either smooth, e. g. in most epidermal layers of branches cited above under No. 1; or it is rendered uneven by numerous small processes, which penetrate the cellulose layer like little teeth. Very small processes of this sort are for instance to be found on the branches of Taxus [9], the leaf of Hoya carnosa; and larger sharp teeth on the leaves of many species of Aloe (Fig. 25), and the phylloclades of Ruscus aculeatus. Epidendron ciliare has numerous fine teeth both on the surface of the cuticular layers which cover the cellulose wall externally, also on the wedge-shaped ridges, which protrude into the lateral walls, and thirdly on their sharp angular pegs, which protrude further into the lateral angles than the

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[1] Compare von Mohl, Verm. Schriften, Taf. IX. X. figs. 12, 14, 23, 26.—Vegetab. Zelle, fig. 40. —Schacht, Lehrbuch, I. Taf. III. figs. 16, 17, 23–25; IV. 9, &c.

[2] Von Mohl, Botan. Zeitg. 1849, p. 593.

[3] Botan. Zeitg. 1871, p. 596.

[4] Wigand, *l. c.* p. 78.

[5] Petunikow, *l. c.* pp. 19, 20, fig. 21.

[6] Wigand, *l. c.* p. 105.

[7] Botan. Zeitg. 1871, p. 577.

[8] Von Mohl, Verm. Schr. *l. c.*—Schacht, Lehrb. *l. c.*—Wigand, *l. c.* fig. 43.

[9] Graf zu Solms-Laubach, Botan. Zeitg. 1871, p. 536.

ridges. On the epidermis of the branches of Prumnopitys elegans[1] the processes are very large, in the form of thick plates, which are blunt, often branched, of unequal size, and irregular curvature; so that in their sections separate pieces, cut off from these, lie isolated in the non-cuticularised membrane. On the leaves of many Proteaceæ (Lomatia longifolia, Hakea ceratophylla, H. Baxteri[2]) the processes are blunt and swollen, and the spaces between them, which are filled with cellulose, are narrow slits. These appear in surface-view as bands which are

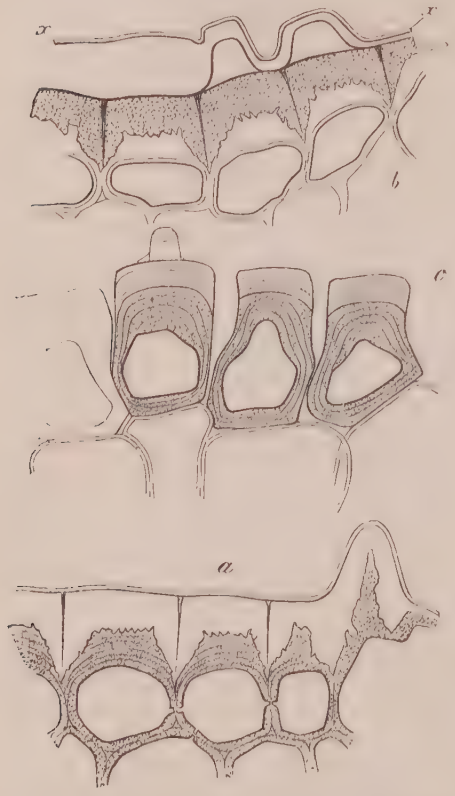

FIG. 25.—(390) Transverse section through the leaf of Aloe verrucosa. *a* lying in water, not acted upon by reagents. The non-cuticularised parts of the membranes shaded; outside this the cuticular layers, broken up by darker limiting lamellæ, and covered by the cuticle, which has a double contour. *b* after warming with potash solution. The cuticle *x—x* raised from the (shaded) cuticular layers; the non-cuticularised (unshaded) inner layers somewhat swollen. *c* epidermal cells after complete removal of the cuticle, and of the cutin deposited in the cuticular layers, by continued boiling with potash. They are separated from one another, and are seated upon the cells of the sub-epidermal parenchyma; the cuticular layers are now only distinguishable from the others by more delicate stratification.

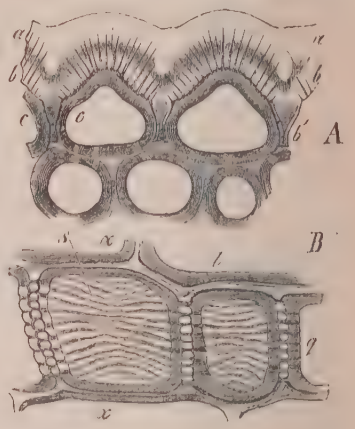

FIG. 26.—(800) Ilex aquifolium; leaf. *A* transverse section through the midrib of the under side; *a*, *b* cuticular layers, the inner (*b*) stains yellow with Schultze's solution, and is continued into the limiting lamella, which reaches to the sub-epidermal layer. The outer (*a*) remains uncoloured in Schultze's solution (only partially true cuticle?). *c*, *c* the non-cuticularised portions of the membranes. From Sachs' Textbook, compare p. 35.—*B* a few cells of the same epidermis, seen from the outer surface.

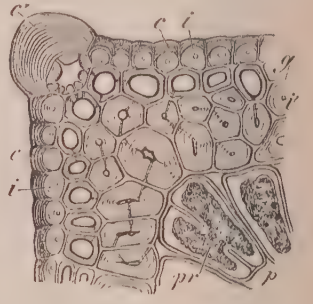

FIG. 27.—(800) Pinus Pinaster. Leaf, transverse section, corner of the margin. *c* cuticularised; *i* inner non-cuticularised layers of the epidermal cells; *c'* very large and thick-walled cells lying at the corner; *g—i'* hypoderma; *p* chlorophyll-containing parenchyma; *pr* contracted protoplasmic body of the cell with infolded walls. From Sachs' Textbook.

[1] Graf zu Solms-Laubach, *l. c.*

[2] Nägeli, Sitzungsber. d. Bayr. Acad. 7. Mai, 1864, Taf. II, 19, 20.

arranged irregularly round one central point, or in the case of elongated cells round two eccentric points. They are often also branched, and connected by anastomosis. In vertical sections they appear as thin bright radial bands. With Schultze's solution they turn blue like outgrowths of the inner cellulose layer, while the cuticular layers with their protruding swellings assume a brown colour. This behaviour causes the doubt expressed by Nägeli in these cases, as to the nature of the above-mentioned slits.

As regards the internal structure of the cuticular layers, we need not here discuss the phenomena of stratification, striation, and areolation, which are general for thickened cell-walls[1]. Different successive layers or systems of layers (shells) are in many cases cuticularised to a different extent, and are therefore of different refractive power and colour differently with preparations of Iodine; e.g. in Ilex aquifolium (comp. above, Fig. 26), Aloe soccotrina, Fourcroya gigantea, Taxus baccata, (Petunikow, *l. c.* Tab. III, Fig. 3, 4, 7, 9). The same holds in many cases for the successive striæ perpendicular to the surface. Hakea Candolleana Meisn. has for instance a quite similar striation to that above described for H. ceratophylla. But the striæ lie in the cuticular layers, and do not extend inwards to the cellulose layer: moreover they turn bright yellow with Schultze's solution, while the other cuticular layers turn brown[2]. Epidendron ciliare shows with Schultze's solution broad striæ, perpendicular to the surface, of variable and very different intensity of colour.

Another phenomenon, also of common occurrence in masses of cells, is the difference in optical and chemical nature of the *limiting layers*, and *limiting lamellæ* of contiguous cells, from the other membranes. And this occurs often very conspicuously in the cuticular layers. Sharply marked, thin limiting lamellæ often extend from the cuticle, tapering off inwards like wedges. They appear like continuations of the cuticle inwards, between the cuticularised lateral walls of many epidermal layers. They also are destroyed by those reagents, which destroy cuticular substance, and therefore consist entirely or principally of it (comp. Fig. 25, *c.* and Fig. 27). In other epidermal layers (e.g. Acer striatum, Dianthus caryophyllus, &c.) limiting lamellæ are not visible or hardly indicated in the fresh intact preparation. But in these cases also the lateral walls of contiguous cells are separated by reagents, which destroy the cuticular substance, and this tends to the conclusion that there is a delicate limiting lamella consisting entirely or chiefly of cuticular substance.

Ad. Brongniart[3] used the term *cuticle* to indicate, in the first place, that superficial homogeneous lamella of the Epidermis which alone remains behind when all the rest is destroyed by rotting or by the action of sulphuric acid. The names of the plants investigated by him show that he did not distinguish the cuticular layer from the cuticle, since after the maceration both of these remain, in the leaf of Dianthus caryophyllus, as

[1] Compare Hofmeister, vol. I of this Handbook, §§ 27, 28.

[2] The striæ described by Nägeli, *l. c.* figs. 14, 15, and Schacht, Lehrb. Taf. III. 27, 28, for H. florida, and by von Mohl, *l. c.* fig. 18, for H. gibbosa, may be compared with those of H. ceratophylla.

[3] Ann. Sci. Nat. 2 sér. tom. I. p. 65. Brongniart's first description was in the Ann. Sci. Nat. 1 sér. tom. XXI. p. 427 (1830).

a connected skin, while in that of Potamogeton lucens only the cuticle remains, since the cuticular layer is absent. The distinction of the two parts was not drawn by the observers of the succeeding period[1]. Mohl first drew attention to their anatomical and material difference (Bot. Zeitg. 1847, p. 499, &c.).

As regards the *cuticular layer*, the view, defended earlier by himself and by Meyen, that the 'cuticle' is part of the outer membrane of the epidermal cells themselves, was distinctly proved in this work of Mohl: and the view held by others (Treviranus, Schleiden, Grundz.), which regarded it as a product of *secretory-perspiration*, was laid aside. Mohl says of the *cuticle*, 'If any one will ascribe it to a secretion from the epidermal cells, I have no objection to make to this idea, still it will be difficult to afford a proof of its truth.' This he confirms by the striation which occurs in many plants, from which it may be concluded that there is a definite organisation, and not an origin merely from hardened excreted fluid. Cohn (De cuticula, in Linnæa, Bd. 23, 1850) then gave a clear statement of the case, founded especially on investigations on hairs. Wigand[2] also claimed for the cuticle a (genetic) connection with the cell-membranes of the epidermis, and defended his view against that of Schacht (Pflanzenzelle, Lehrbuch I), which is certainly confused. Hofmeister regards it as a part of the cell membrane of the epidermis[3].

If, in the face of the facts known at that time, most of which are recapitulated above, the question be raised whether the cuticle consists of parts of all epidermal cells, or is something distinct from these, the latter alternative must be preferred, even if anatomical relations alone be regarded, and the difference of material be left on one side[4]. Even if Payens'[5] statement were confirmed, according to which the cuticle of Cereus peruvianus, after continued treatment with boiling nitric acid, water, and ammonia, if pressed backwards and forwards under the cover slip, separates into angular pieces, each corresponding to an epidermal cell; still this is only an isolated exception. Universally in other cases the cuticle, having been first formed on the embryo, while still consisting of few cells, grows over the epidermal cells, and uniformly with them, retaining fundamentally its original properties. Neither in older nor in younger parts can it be separated into the altered outer lamellæ of single epidermal cells, or groups of cells. Even if it, together with the membranes covered by it, consisted of pure cellulose, it would be, anatomically considered, an independent membrane, which belongs in common to the whole member or the whole plant, and must be distinguished from the walls of the single cells. Its genetic relationship to the contiguous cellulose layers is not thereby excluded; it must rather be directly derived from them in all cases where it grows or is renewed on a free surface, that is, in those cases where the possibility of an apposition from without is excluded (e. g. such a possibility may be imagined for the embryo enclosed in the embryo-sac). Further, if we neglect the embryos, pollen-cells, &c., it is possible on free surfaces—in the development of the stomata—clearly to observe that first the cellulose membrane alone is present, and later the cuticle appears upon it. Thus, where reference can be made to the first beginnings of the development of cuticle (comp. Hofmeister, *l. c.*), at first the cellulose membrane alone is present, subsequently it is separated into cuticle and cellulose membrane. Where the cuticle grows on a free surface, the material for it can originate only from the cellulose membranes. It is therefore doubtless a *product of differentiation* of these, and of the cells to which they belong.

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[1] Treviranus, Physiol. I. p. 448.—Meyen, Physiol. I. p. 176.—Von Mohl, Linnæa, 1842, and Verm. Schriften, p. 260, &c.

[2] Intercellularsubstanz und Cuticula. Braunschw. 1850, p. 36, &c.—Botanische Untersuchungen (1854), p. 67.—Flora, 1861, p. 81, &c.—That which is said in these works of the Intercellular substance does not of course concern the present explanation.

[3] Pflanzenzelle, p. 159, 248, 257, &c.

[4] Compare Cohn, *l. c.* p. 382.

[5] Compare Hofmeister, *l. c.* p. 251.

The cuticle differs from the cell-membranes in its material composition: it consists at all events in the main of cutin, even though Hofmeister's[1] observation that the cuticle of Orchis Morio and Hoya Carnosa, after maceration for three weeks in potash, became 'distinctly' blue with solution of I in K I should prove that cellulose was present (*though this point will not be conceded*). The question then arises, what is the origin of cutin, from what material, and where is it produced? Since it can only originate primarily from the epidermal cells, and appears originally on the apparently pure cellulose membrane, and later also is seen within this, in the cuticular layer, and since it is never found in the protoplasm and cell sap, its origin *in* the cellulose membrane and from cellulose is probable, though a safe proof of this cannot be drawn from the facts at our disposal.

It need not here be emphasised that the cuticle is separated from the very first as a sharply defined lamella, for which a definite structure from the very first may be assumed; and that the old view, which, in cases of excretion or secretion, imagined a fluid mass filtered out, and hardened sooner or later, is here as little apposite as is the case with most of the other 'secretions.' Comp. Sects. 17, 19.

As regards the origin of the cutin which impregnates the cuticular layer of the cell-walls, the same holds as has been said for the cuticle. Relatively to the formation and growth of this layer, it may certainly be observed in many cases (which should moreover be more carefully studied) that a progressive cuticularisation of the cellulose membrane proceeds gradually from without inwards; thus in the above-cited examples of Psilotum and Selaginella. But in the overwhelming majority of cases—on which, however, still more thorough investigation is necessary—e. g. leaves of Agave Americana[2], species of Aloe, branches of Acer striatum[3], the cuticular layers are first formed with their definitive sharp outline as thin lamellæ, and grow as cutin-containing layers till they attain their definitive thickness, being always sharply marked off from the cellulose layer which grows with them. It may be thought that their increase depends on cuticularisation which progresses inwards, but this is not evident on observation.

The opinion of Hartig and Karsten[4], according to which the cuticle is a development from the mother-cell-wall of the plant, has hardly any longer a historical interest in the face of what we now know, especially concerning its restoration, its entry into the stomata, and concerning the internal cuticle.

The chemical composition of the body called cuticular substance, or, after Frémy, cutin, which forms the cuticle, and is contained in the cuticular layers, is not yet quite clearly known. It is indeed very probable that we have not in all cases to do with the same body, that for instance important differences exist between the deep-brown coloured substance of the cuticularised epidermis of Ferns, and the colourless or slightly coloured cuticular substance of the epidermis of Phanerogams. Investigations on the body in question refer almost exclusively to the latter. On the ground of Payen's[5] works, the cuticular substances were regarded as nitrogenous bodies—products of the change of cellulose by combination with a nitrogenous compound.

Frémy[6] isolated the cuticle of various leaves, parts of flowers, and fruits (Iris, Camellia, apples), and found the elastic, extensible skin, which retained its original structure

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[1] Pflanzenzelle, p. 257.

[2] Compare Oudemans, Mémoire sur les stomates, &c.; C. Rend. de l'Acad. d'Amsterdam, vol. XIV.

[3] Compare Botan. Zeitg. 1871, p. 596, Taf. II. figs. 29–35.

[4] Botan. Zeitg. 1848, p. 730.—Compare Hofmeister, *l. c.* p. 251.

[5] Details in Hofmeister, *l. c.* p. 249, &c.

[6] Comptes Rendus, tom. 48, p. 669.—Ann. Sci. Nat. 4 sér. tom. XII. p. 331.—On Payen's replies to Frémy compare Comptes Rendus, tom. 48, p. 893. Further, the revision of the discussion in point in Kopp and Will, Jahresbr. ü. d. Fortschritte der Chemie für 1859, p. 529, &c., especially pp. 536, 539.

after boiling with dilute hydrochloric acid, and subsequent successive treatment with ammoniacal sub-oxide of copper, hydrochloric acid, potash, ether, and alcohol, to be non-nitrogenous, consisting of the body which he calls *cutin*, and for which he gives the following percentage composition—C, 73, 66 . H, 11, 37 . O, 14, 97. The cutin shows the properties above described (p. 74). When heated it gives fatty acids, on treatment with boiling nitric acid, suberic acid, and may be saponified by boiling with concentrated solution of potash. The cuticle and cuticular layers of the leaf of Agave Americana, after their isolation by Frémy's method, appeared to me to have retained their structure completely: they still retained traces of cellulose which could be determined microchemically. An analysis completed once in Halle, in Professor Stohmann's laboratory, showed the substance to be *completely* non-nitrogenous.

Sect. 17. In company with the cuticular bodies there are usually found compounds of a *waxy* nature, i. e. carbon compounds, the chemical constitution of which requires, it is true, more careful investigation, and perhaps is not very closely allied to that of bees-wax, but which in their physical properties as now known, such as solubility, fusibility under 100°, &c., resemble the better known sorts of wax, and therefore may for the present be shortly termed *wax*. As regards their solubility, all the allied waxy bodies are soluble with difficulty or not at all in cold alcohol, but completely in boiling alcohol. Most of them, but not all, dissolve in ether even without any considerable rise of temperature. According to the incomplete investigations hitherto made, many sorts of wax found on the epidermis prove to be mixtures of two or several bodies: with many there is mixed a considerable quantity of resin, easily soluble in cold alcohol, e. g. with the wax of the stems of Ceroxylon, Klopstockia, and Chamædorea; a compound of Silicon is mixed with others (stems of Chamædorea and Kerria) [1].

Wax is not present, according to the existing investigations, in the epidermis of parts which are submerged, or underground. In epidermal layers however which are surrounded with air it occurs very generally, perhaps even universally, partly *imbedded* in the cell-wall, partly *extended* on the outer surface of the cuticle as a *wax-covering*.

Imbedded wax occurs only in those walls which consist of or contain cutin, and not in the relatively pure cellulose membrane. It is found both in those which simultaneously extrude wax-coverings, and also in others in which the latter are absent or only very slight, such as the stems and branches of Acer striatum, Sophora japonica, Jasminum fruticans, the foliage leaves of Cycas revoluta, Aloe verrucosa, Epidendron ciliare, Hoya carnosa. The imbedded wax is disposed in the cuticular membrane in the form of small bodies, which, in fresh preparations, cannot be recognised optically. It is determined anatomically, by fusing it out of the sections by carefully warming them in water. It then exudes from the cuticle and cuticular layers in the form of small drops. Boiling alcohol extracts it from the membranes. The latter, after the wax has been fused or dissolved out, retain their original structure. But where the infiltration of wax has been excessive (Acer striatum, Klopstockia) their volume is considerably reduced, the reduction remaining even after subsequent treatment with water.

[1] On the composition of the bodies in question, compare Wiesner, Botan. Zeitg. 1876, p. 225, postscript.

Wax-coverings are extruded on the outer surface of the cuticle in four chief forms, which may be described as (1) *strata* or *crusts*, (2) *rod-like coverings*, (3) *simple granular layers*, (4) *aggregated coverings*.

The *strata* or *crusts* are superposed on the cuticle in the form of a continuous membrane. On many epidermal layers they form a clear, smooth, brittle *glaze*, which, when the epidermis is stripped off, appears cracked and broken into angular pieces. It attains a thickness of about 1μ. Thus on the foliage of Thuja orientalis, occidentalis, of Sempervivum tectorum, calcareum, the young stem of fleshy Euphorbias (E. Caput Medusæ L., E. ornithopus, E. canariensis, piscatoria, balsamifera Ait.[1]), of Lepismium paradoxum Salm., Kerria japonica. Very delicate, angular, homogeneous scales, like the fragments of a delicate skin of wax, are also found as a rudimentary form of the glaze on many smooth shining epidermal layers: Cereus alatus, species of Opuntia, leaf of Fuchsia globosa, Taxus baccata, leaf and stem of Portulaca oleracea.

In other cases the wax-layers attain very considerable thickness and then show a more or less complicated structure, stratification parallel to the surface, and a striation or areolation, or both of them together. The wax-crust of Euphorbia canariensis on old branches attains a thickness of 70μ, and shows obvious stratification: that of Kerria is more than 5μ thick, and is also stratified. The stems of species of Chamædorea, especially Ch. Schiedeana, Mart., are covered by a stratified glaze of wax up to 14μ thick, which is brittle, and contains silica. The wax covering on the epidermis of the stem of the wax palms of the Andes, Ceroxylon and Klopstockia, are much more massive, attaining a thickness of 5^{mm}, and show rich stratification and areolation. The young leaves of Corypha (Copernicia) cerifera are covered on both sides by a wax-layer which is also striated perpendicular to the surface, but attains a thickness of only 15–19μ. This having crumbled off from the dried leaf, is collected as Brasilian Carnauba-wax. The stems and leaves of Panicum turgidum, Forsk., are covered by a crust of wax up to 30μ thick, which is brittle and striated perpendicular to the surface.

The thin glaze of wax, of the leaves of Sempervivum glaucum, which is in other points like that of S. tectorum, is warty and uneven on its outer surface; that of the leaves of Cotyledon orbiculata, L., is studded with numerous erect converging out-growths in the form of rods 10μ high, and about 1μ thick.

The latter form the transition from the form of wax-covering above described to the *rod-like-covering*, which covers the epidermis of the under surface of the leaf of Aechmea farinosa, but occurs especially in many Scitamineæ and Gramineæ: e. g. on the under surface of the leaf, and on the petioles of Heliconia farinosa, Strelitzia ovata (Fig. 29), Musa spec., on hypsophyllary leaves of species of Canna, internodes and nodes of Saccharum officinarum (Fig. 28), Eulalia japonica, Trin.; on the short slightly silicified epidermal cells on the leaf-sheaths and the under surface of the lamina of the latter species, further in the same positions, and on the stems of species of Sorghum, Coix lachryma, &c. Rods consisting of wax here stand perpendicularly upon the cuticle, either at relatively wide distances apart (distances equal to or greater than their width), or so near one another as even

[1] Schacht, Lehrb. II. p. 559.

to touch. The rods may be as high as the epidermal cells (Strelitzia, Internodes of Saccharum, &c.) or in most cases much higher,—the longest, especially those observed on the nodes of Saccharum, attain a height of more than 100μ and 150μ. Their height is however very unequal. Their thickness reaches usually on the average about 1μ, but in the largest often three or four times as much. Their form is cylindrical, or, in the case of the thickest, more or less angular or compressed like a riband. They are straight in their lower part, which is attached to the epidermis, but the upper ends are, in the shorter ones, hooked, in the longer ones very strongly curved like a crosier, or a cork-screw curl. Their substance is homogeneous, or, when they are large, longitudinally striated. To the naked eye the rod-like coverings appear as a white mealy covering of the surface varying in mass according to the size and number of the rods, and easily scraped or brushed off. It is most

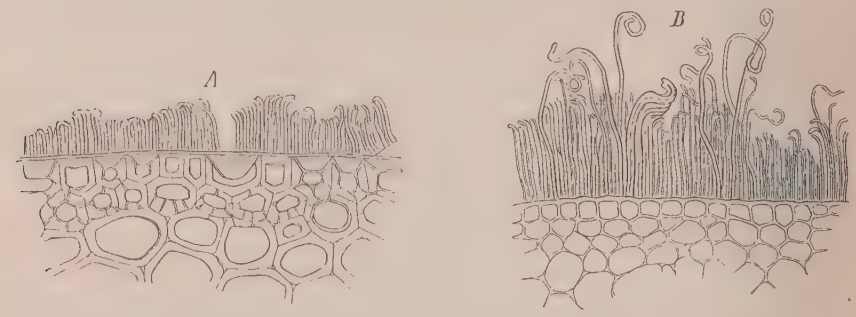

FIG. 28.—Transverse sections through the stem of Saccharum officinarum. *A* (375) surface of a mature young internode, *B* (142) of a similar node.

obvious on the leaves of the Heliconia above cited, and on the nodes of Saccharum.

That form of the covering is termed a *simple granular layer* in which granules of wax are superposed on the cuticle, side by side in a simple layer, and not heaped upon one another. The granules have on the average a size up to 1μ: they are spherical, or in the form of very short rods perpendicular to the surface (e. g. Allium fistulosum, branches of Acer striatum), and form, when of the latter shape, the transition to the rod-like coverings. They lie either at wide distances apart (e. g. upper surface of the leaf of Tropæolum majus, Begonia semperflorens and other spec., Vitis vinifera), or they approach one another leaving small spaces, or till they touch one another, the latter, e. g. in the mature leaves of Tulipa, Echeveria pumila, and other species, Dianthus caryophyllus, the red and white cabbage, &c. When the granules are not too far distant from one another they form the white or blue, easily removed bloom, to which so many so-called glaucous parts owe their character. Of the innumerable examples of this besides those already cited may be named the parts of the epidermis of the above-cited grasses, which do not bear rods, the leaves of Iris germanica, pallida, Galanthus nivalis, Allium, Brassica oleracea var., Mesembryanthemum spec., Calandrinia speciosa, the upper part of the inner side of the leaf-pitcher of Nepenthes (Wunschmann, *l. c.*).

A large number of glaucous and hoary parts of plants from the most various families are covered with the wax-bloom of the fourth type, which is termed an

aggregated wax-covering, since it consists of an aggregation of very delicate rods or granules, which cover the cuticle not with a simple layer, but with several irregular layers. Examples of the aggregated rods are found on the white Eucalypti (E. globulus, pulverulenta), Acacias (A. Hügelii, cultriformis), Lonicera implexa Ait., Andromeda dealbata; Secale cereale, Elymus arenarius, Encephalartos horridus; examples of aggregated granules are found on Kleinia ficoides, Ricinus communis, under surface of the leaf of Abies pectinata and its allies. Intermediate forms between the third and fourth type are sometimes found, e. g. leaves of Agave Americana.

The wax-coverings usually cover the whole epidermal surface evenly, or with the differences of form described above for the epidermal cells of differing contour. The granular and aggregated coverings also overlie the guard-cells of the stomata up to the entry of the slit. The stratified coverings, where observed, leave the stomata free, in so far as they belong to parts already unfolded, or at least they become so thin as to be unrecognisable over the guard-cells. On the other hand the wax-layer of the young not yet unfolded leaf of the Carnauba palm completely covers the stomata also:

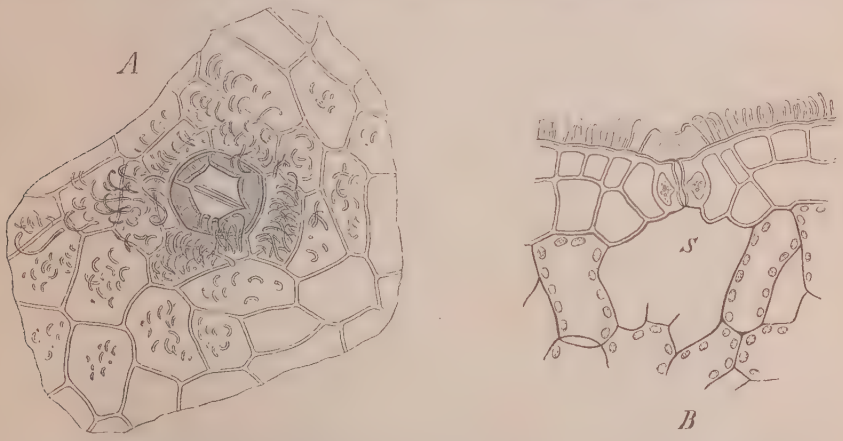

FIG. 29.—Strelitzia ovata. *A* under surface of a leaf still in course of unfolding; on the epidermal cells are rods of wax in course of growth; surrounding the stoma is the striated ring.—*B* transverse section of a mature leaf. Epidermis with one stoma (lying above the wide respiratory cavity *S*), the rods and the ring. Under the epidermis is the large-celled hypodermal layer; below this the chlorophyll-containing cells of the leaf parenchyma (375).

these however are freed when the leaves unfold, since the spontaneous crumbling off of the wax-layer on the unfolded leaf, though not indeed directly observed, may still be certainly assumed from the data at our disposal. Certain of the Scitamineæ show remarkable peculiarities in the distribution of the rods. On the leaf of Musa ornata the short rods are situated chiefly, if not exclusively on the edges of the epidermal cells. Strelitzia ovata (Fig. 29) has rods distributed over the whole lower leaf-surface. Those which stand on the annular rows of cells surrounding a stoma converge with their hooked ends towards the stoma, and on the edge of the wall, which separates the two half-moon-shaped subsidiary cells from the surrounding epidermal cells, stands a ridge consisting of wax, and having the form of a ring diminishing conically outwards, with its margin curved inwards, and with radial striation, which gives it the appearance of being composed of many converging crosiers. The outer surface of the subsidiary cells themselves, and of the

guard-cells, is free from wax-covering, the stoma is as it were shut off from this by the ring. Other species of Strelitzia have a similar ring, though in form and distribution of rods they differ from S. ovata.

The structure and development of the wax coverings and intramural wax have been described by the author of this book in a longer treatise (Bot. Ztg. 1871). There also the very limited older literature on this point is quoted. Later Wiesner made two additions (Bot. Ztg. 1871, p. 769). For various details we must refer to these special works. We can here add but little to what has been said above.

The internal structure of the wax coverings, which in the rods is indicated by the striation, i.e. by the presence of longitudinal layers of alternately unequal optical properties, attains in the thick layers a complicated differentiation. In the investigated material of Klopstockia cerifera Karst. (Fig. 30) the covering attained a thickness of 0.66 mm. Above each stoma it is perforated by a perpendicular canal S–S' which contains air and fungal hyphæ. It is composed of prismatic pieces, of which each fits exactly over one epidermal cell, and which are not arranged separately side by side, but are connected directly by a homogeneous intercalary or fundamental mass. This appears in thin sections as a transparent limiting band between the sides of the prisms. Each of the latter shows internally (1) a rich and delicate stratification parallel to the outer surface of the contiguous epidermal cell, dark and clear layers alternating, of which the latter resemble the hyaline limiting bands; (2) darker longitudinal bands perpendicular to the strata and to the surface, these are denser the nearer they run to the lateral surfaces of the prism in the hyaline substance; (3) delicate striations which run from the lateral faces obliquely at an angle of 30°–40°, slightly curved, towards the epidermis and the median line of the prism, but do not reach the latter. Under a low power they are not seen, while the longitudinal striations are only slightly visible, the strata appearing to be continuous from one prism to the other: as in Fig. 30.

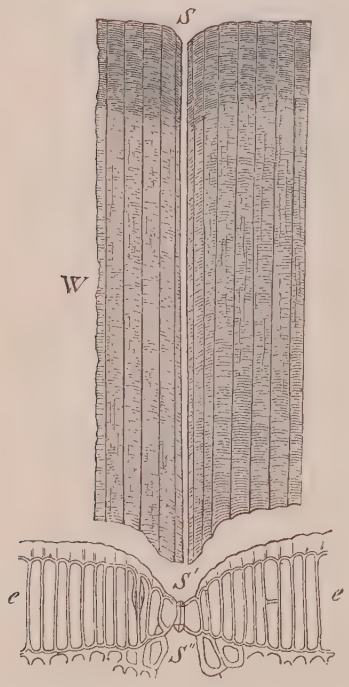

FIG. 30.—(116) Klopstockia cerifera; internode of stem, transverse section. *e*—*e* epidermis; *S*—*S''* stoma, with two small guard-cells between the two larger subsidiary cells; *w* wax covering over the epidermis, over which it fits; *S*—*S'* the canal leading to a stoma.

The deposits of wax on species of Chamædorea, Euphorbias, Panicum turgidum, and the fruits of Myrica cerifera, show striation and stratification of a simpler sort. The wax covering of the fruit of Benincasa cerifera is peculiarly complicated; it consists of a reticulate layer, and bundles of rods united across one another like a trellis.

The layer of wax on the young leaf of Corypha cerifera was first described by Wiesner (*l. c.*), and, as I think, not correctly in all the particulars. I find in the material which I received through the kindness of Professor Wiesner the following structure. Both leaf-surfaces are covered by a white layer, in which there appear under a higher power three constituent forms: (1) a clear transparent ground substance; in this (2) dark (blueish) spots, and (3) much clearer more transparent points in the form of very various figures, sometimes narrow slit-like, sometimes round. The latter clear spots appear as cavities in the substance, and may here be so called. Thin transverse sections

show that they correspond to deep tube-like depressions of the surface, but these are not complete perforations: it must remain undecided whether such perforations may occasionally occur. The three constituents are unequally distributed in correspondence with the longitudinal bands with and without stomata, which alternate in the leaf-surface. On the former the holes are very near together, and numerous: the spots between them form a narrow very irregular net, the substance of which has chiefly the darker, blueish appearance. The network is densest and the meshes narrowest over the stomata themselves, i. e. over the pair of guard-cells: a narrow slit-like hole corresponds usually, but not always, to the slit of the stoma. On the bands of the leaf without stomata, the wax-layer is more homogeneous: it has more solitary usually slit-like holes.

Corresponding to these appearances of the surface view, the transverse section of the wax-layer shows straight bands, of alternating unequal refractive power, which are parallel and perpendicular to the surface. The clearer parts correspond partly to the holes, partly to the more transparent fundamental mass. On the parts which have many pores and stomata, the striation is, as might be expected, much denser and more clearly defined than on the parts with no stomata. But figures, like Wiesner's Fig. *b*, I have never seen, at all events not on clearly cut sections. It must finally be added to the above typical description, that the regions distinguished are not always quite sharply limited from one another. Again, Wiesner's description of the wax of the sugar-cane corresponds so imperfectly with the appearances found on fresh plants, that the idea suggested itself of different structure of the covering in different sorts or varieties. My observations on material, also kindly supplied by Wiesner, on which his statement was founded, do not confirm me in such an assumption. The traces of dense, normal rod-structure may be clearly recognised, and are made indistinct by all sorts of injury (especially very many fungal hyphæ are present), just as one may observe it on the old nodes of living plants (comp. Bot. Ztg., *l. c.*, p. 151). Wiesner's statement that the wax layers and rods appear doubly refractive under polarising apparatus is quite correct; the same holds for wax-deposits, which I investigated on this point: my only reason for not mentioning this earlier, was that it appeared to me to afford no decided conclusion concerning the nature of the layer.

As regards the development of the wax-layers, it is proved that they appear on the persistent cuticle, and that they are extruded, and do not owe their origin to a metamorphosis and metacrasis of the cuticle and cell-membrane itself, as earlier writers had asserted (Wigand, Karsten, Uloth). Wax-layers may arise from very dense simple granular coverings, by lateral fusion of the granules as they increase in number and size. The typical layers arise in the first place as such: they may follow, by intussusceptive growth, the increase of girth of the part which bears them (Kerria, Euphorbia, Chamædorea). The coverings appear, either when the part which bears them is very young (Eucalyptus, Acacia, Dianthus, Echeveria, Carnauba palm), or only in later stages of development, e. g. not till the unfolding of the bud (leaves of Strelitzia, Heliconia, Galanthus, Tulipa, Cotyledon orbiculata, stem of Saccharum, Chamædorea, fruits of Myrica, Benincasa). Cases of the latter sort should be chosen for studying the development. The extruded wax may first be determined in the cell-wall, or cuticle, and *emerges from* the latter on the surface: in no case can a trace of wax be found previously formed in the interior of the cells which secrete it, so as to be transmitted outwards *through* the membrane.

The granular and rod-like coverings form that bloom or rime on surfaces which is so easily wiped off. After it has been wiped off it can be renewed[1], provided the part of the plant has not passed a certain stage of development, which must be specially determined for each special case. As far as experience goes, the renewed covering has the same structure as the primary one, but is less massive.

[1] De Candolle, Physiol. p. 233.—Treviranus, Physiol. II. p. 44.

Sect. 18. To the cuticular structures and deposits should be appended the cellulose covering, which was found by Pfitzer[1] on the stems of Restio diffusus, but which was absent from other allied species, and of which the development cannot as yet be explained. On the outer surface of the firm large-celled cuticularised epidermis of this plant lies a colourless, almost homogeneous, and transparent, brittle, dry, easily separated layer, as thick as a strong outer epidermal wall. The layer does not enter the deep hollows in which the stomata lie, but it is rather curved over the opening like a bridge, and closes it with exception of a very narrow longitudinal slit with toothed margin. Beneath the layer lies the cuticle: the layer itself shows an exquisite cellulose reaction. According to careful investigation of the unfavourable material at his disposal, Pfitzer arrives at the very probable conclusion that this layer covering the cuticle is the disorganised outer layer of cells of an epidermis consisting of two layers (excepting in the vicinity of the stomata): a view which is especially supported by the fact that the covering appears in surface-view partitioned off by delicate lines in a cellular manner.

Sect. 19. **Dermal glands.** In the cell-walls of the epidermis there occur very generally distributed resins, ethereal oils, and mixtures of both; and mixed with these also, though more rarely, vegetable mucilage (Bassorin, which swells greatly or is dissolved in water), gum and sugar. When free these substances give to the surface a sticky character; when they are volatile they are perceived as scents.

In contrast to the formation of wax, the occurrence of these bodies is relatively seldom extended over large epidermal surfaces; on the other hand they are usually localised, partly on circumscribed spots in the level epidermis or on teeth or other emergences, most commonly on hair-structures[2].

The spots on which the sticky or volatile bodies in question occur are called in common speech *glands*, *glandulæ*, and the character of surface resulting from these *glandular*, the bodies themselves the *secretion*, or the product of secretion, or segregation of the glands. But this expression is also used for other very different organs, which doubtless correspond partially with those in question in the general characters of the secretion, but differ widely as regards their structure. The organs of the epidermis, usually termed collectively glands (with few exceptions to be treated of later), are characterised by very definite anatomical properties, and should therefore be designated by a definite general name, and be distinguished from the rest. They may therefore be termed *epidermal* or *dermal glands*. According to the above-indicated difference in the distribution and extent of the glandular properties we may distinguish between *glandular hair-structures* (*glandular hairs, scales and villi*) and *glandular surfaces* or *areas* (*glandular surfaces, glandular spots*). When the latter are localised on definite emergences, it is convenient and practical to speak of glandular emergences (*glandular-teeth* or *-warts*, &c.).

The secretion of dermal glands, when it can be recognised anatomically, always appears first in the walls of the cells, and gives them a peculiar structure. In most cases this affects the free outer wall of the cells entirely, or partially: here there appears a bladder-like swelling, hence *bladder-like dermal glands*. In other cases the

[1] Pringsheim's Jahrb. Bd. VII. p. 564.

[2] As regards the literature, the references on p. 57 should be compared.

secretion appears in the walls between neighbouring cells: these may be called glands with intramural secretion, or shortly *intramural glands*. Besides those which result directly from the presence of the secretion there are in most, but not in all cases, other peculiarities of form and structure connected with glandular cells.

(*a*) *Bladder-like dermal glands.* The peculiarity of structure of the bladder-like glands consists in the appearance of the secreted body at the limiting surface between cuticle and cell-membrane. While the form and turgescence of the cell remain the same, the secretion, as it increases in quantity, raises up the cuticle like a bladder: either the cuticle grows simultaneously, while its thickness remains the same or increases, or its surface growth does not keep pace with the increase of the secretion, and hence it becomes strongly stretched, and at last is easily burst. The stickiness of the surface arises from the fluid secretion thus set free by the bursting of the cuticle. The rent cuticle, according to Hanstein, may be repeatedly renewed on young parts.

These phenomena are best seen in the *glandular hairs*. According to their external development these belong for the most part to the capitate form, and the

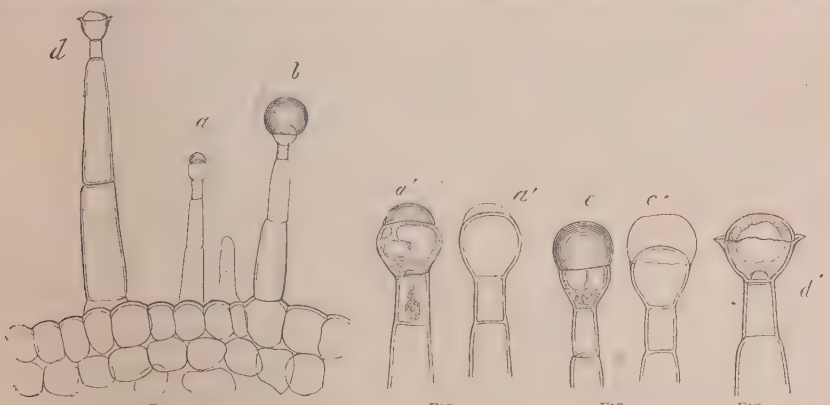

FIG. 31. FIG. 32 FIG. 33. FIG. 34.

FIGS. 31—34.—Glandular hairs of the petiole of Primula sinensis. Fig 31 (142). In *a* the secretion beginning, *b*, with a large secretory bladder; *d* an old hair, the bladder has burst and the upper part disappeared.—Figs. 32—34 (375) Fig. 32 = *a* of Fig. 31. *a'* with intact secretory bladder lying in water; *a''* after solution of the secretion in alcohol. Fig. 33. *c* end of hair, intact; *c'* the same after solution of the secretion by alcohol. Fig. 34 = *d* of Fig. 31 under higher power.

position of the glandular structure and secretion is at the head. When the latter is the expanded head of a unicellular hair, e. g. on the leaf of Aspidium molle[1], or the terminal cell of a compound hair, e. g. leaves of Primula sinensis (Figs. 31 to 34), Pelargonium zonale, Pogostemon Patschouli, &c., its membrane is equally thick all round, delicate and surrounded by the cuticle which is also thin. At the apex there then begins a thickening of the wall which gradually increases in strength and in extent from the apex backwards, spreading over the apical half of the head (Primula sinensis), or even further backwards, and attaining in the Ferns above-named the strength of a firm cell-wall, and in Primula and Pelargonium the bulk of a thick cap, which even exceeds the apical cell in size. The thickening of the wall consists from the first of the resinous body, which, as shown when burst,

[1] Also the teeth of the Paleæ of Aspidium filix mas, and, as an exquisite example, the glandular hairs which occur in this and allied species in the intercellular spaces of the Rhizome.

and treated with dissolving reagents—e. g. alcohol or ether—is intercalated between cell-membrane and cuticle.

The same phenomenon, in the main, occurs in the multicellular heads of the bladder-like glandular hairs, villi, and scales. The thickening by the secretion begins in these cases at a point more or less near the apex of the whole (not on each or on several single cells) and extends from this point centrifugally, varying greatly in extent and bulk according to the special cases. The outer walls of the single cells thus form with one another either a smooth, even, or domed surface, or they arch outwards like papillæ into the secretory mass which overlies them, and is in its turn bounded by the cuticle. The raised cuticle itself is usually homogeneous and structureless, in other cases (shield-like scales of Humulus, Ribes nigrum) it is marked off into areas corresponding to the lateral limits of the cells. As already intimated the glandular structure in hairs is not always restricted to the head; it may also occur on the lateral wall of capitate hairs, and of such as are not capitate as in Cistus. (Fig. 36.)

From the point of insertion of glandular hairs in the buds of Rumex, Rheum, Cunonia, Coffea, Alnus, Carpinus, Corylus, &c., the glandular structure of the walls extends over the smooth epidermis (Hanstein, Bot. Ztg. 1868). This attains thereby the properties of the *glandular surface*. The same occurs in exquisite form on the sticky young shoots of Betula alba (Fig. 35), where the glandular nature of the wall of the shield-like glandular scales extends over the whole epidermis, as far as the ridge of entry of the stomata, where it ceases. The sticky zones under the nodes of Lychnis viscaria and other Sileneæ appear to be of the same nature, but require more careful investigation.

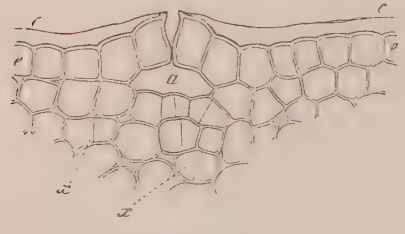

FIG. 35.—Transverse section through a young internode of Betula alba (375). *c*—*e* epidermis; *a* respiratory cavity under the stoma; *c* the cuticle raised from *e*, by a secretory layer, as far as the entry of the stoma (secretion removed by alcohol).

Limited, bladder-like glandular surfaces, that is *glandular spots*, in the above-defined sense (neglecting the nectaries of flowers, which will not be here treated of), occur in solitary cases on smooth surfaces, as on the under side of the leaf of Prunus lauro-cerasus, Clerodendron fragrans, or on the ends of emergences without vascular bundles, as the capitate ends of the villus-like prickles of Rosa[1], the glandular warts of the branches of Robinia viscosa[2]; but the principal place of their occurrence is on leaves and leafy parts over peripheral *endings of vascular bundles*, sometimes on the surface, sometimes on parts of the epidermis which overlie emergences and teeth of various form and arrangement: as examples may be mentioned, the glandular teeth of the margin of leaf-laminæ, e. g. species of Prunus, Salix, &c.[3], the various 'glands' of the leaf-organs of the Malpighiæ[4], and species of Acacia[5] and many others[6].

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[1] Rauter, *l. c.* p. 30.

[2] Meyen, Secretionsorg. Taf. VI. 7–12.

[3] Compare Treviranus, Physiologie, II. p. 6.

[4] A. de Jussieu, Monographie des Malpighiacées, p. 92.

[5] Unger, Flora, 1844, p. 703; Anat. und Physiol. p. 362.

[6] Numerous examples of this have been recently described by Reinke, in Pringsheim's Jahrb. Bd. 10, p. 119 (Nachtr. Anm.).

On those parts which have a glandular surface only in their younger stage, as Rumex, Betula, &c., the epidermal cells of the glandular surfaces are not distinguished by peculiarities of structure. On the sticky zones of the Silenæ between the ordinary epidermal cells there are others, which are characterised by special form and dark granular contents, to which alone Unger attributes the excretion of the glutinous substance. In Silene nemoralis[1] these are simple, broader cells, slightly curved outwards like papillæ: in Lychnis viscaria[2] they are very short hairs consisting of one small pedicel cell, and one roundish apical cell which rises only slightly above the epidermal surface.

These circumscribed glandular areas have the common peculiarity, that their epidermal cells are richer in granular protoplasm, smaller, and more delicate than those on the rest of the dermal surface, and are of the form of elongated prismatic or narrow pyramidal bodies with the longer axis standing perpendicular to the surface. In Passiflora spec. the prismatic cells are divided by a transverse wall into two nearly equal halves: the glandular epidermis thus consists of two layers. In Clerodendron fragrans also there are two layers, the inner consisting of angular tabular cells with very thick lateral walls, and the outer of narrow prismatic cells, which are at least sixteen times as numerous. It is obvious at first sight that in all cases the narrow prismatic cells result from repeated division of the primary epidermal elements, and that the structures in question are morphologically allied to the scale-like hair-structures. In fact there exists between the glandular area of Clerodendron fragrans, and a group of the laterally united top-shaped scales of Hippuris or Catalpa, only this one important difference, that the latter are placed above, the former in the epidermis. The glandular area on the leaf-tooth of Mercurialis annua may, as regards its form and articulation, be also termed a top-shaped scale, &c.

b. The intramural glands, in which the product of secretion appears in the limiting wall between the cells, are obviously always multicellular. They rise as scales, capitate hairs, or villi above the outer surface, or they do not rise above it, but rather intrude as *depressed glands* into the subepidermal tissue. The connection with the bladder-like forms is effected by the villi of buds found by Hanstein in many plants, in which the resinous secretory layer appears both under the cuticle of the outer surface, which is raised like a bladder, and on the limiting surfaces of the lateral and inner cellulose walls (Azalea indica, *l. c.*, Figs. 93–95). In the typical allied forms no secretion occurs between the outer wall and cuticle, but only on the limiting surfaces of the division walls. The latter are finally separated by a voluminous secretory layer. The cells, which in the known cases are narrow and elongated, stand in the secretory mass like the rods of a trellis or the pillars of a vault.

Of the allied hair-structures, which protrude outwards, may be named the large capitate glandular hairs of Ledum palustre: the flat top-shaped glandular scales of the under surface of the leaf of Rhododendron ferrugineum, hirsutum (Fig. 41), Caucasicum. Further investigation will probably increase the number of examples of this class. Those bodies which appear to the naked eye as bright round points on both surfaces of the leaf of many species of Psoralea (Fig. 42; e. g. P. bituminosa,

[1] Unger, Grundlinien, p. 82.

[2] Idem, Anat. und Physiol. p. 214.

hirta, stricta, pinnata, verrucosa, &c.[1]) are imbedded intramural glands; to the structure of these attention had been drawn by Hildebrand[2] in a description which is not quite correct.

If we compare the use of the word Gland by the different authors, and ask ourselves what is really called a gland, we come to the conclusion that this name implies any part of the plant from which something does or may come out, or in which something is contained which, according to the conception of the author, is distinct from those bodies which together form the generally distributed plant-substance which no plant is without, as e. g. cellulose, starch, chlorophyll, &c. A consistent distinction does not exist, since the *point of excretion* of the most heterogeneous bodies—air, water, calcium salts, resin, sugar, &c.—of the most varying structure—epidermis, hairs, stomata, ends of vascular bundles—and *points of deposit*, which are as variable in contents and structure, viz. cells, groups of cells, intercellular spaces, are arbitrarily termed glands or not. Compare e. g. Meyen, Secretionsorgane; Treviranus, Physiologie, II. p. 1, &c.; Unger, Anat. und Physiol. pp. 209–215; Martinet, Ann. Sci. Nat. 5 Sér. XIV.

The facts which underlie this confusion of glands are, taken impartially, in the main the following. At definite points, especially above the ends of vascular bundles, water-pores, &c., water coming from below filters out on the surface, and bodies, such as sugar, gum, salts of calcium, may occur in solution in it: the water gives the surface a moist character, or evaporates and leaves the dissolved bodies behind as a solid excretion.

Secondly, the surface may be moist, or sticky, or incrusted by bodies, which issue directly from the epidermis itself, as e. g. the resin of the glandular hairs.

Thirdly, both the above processes may combine on one and the same surface, as e. g. on the glandular spots of the Acacias.

The same bodies, which make the surface moist, or sticky, occur, in the fourth place, also in the interior of the tissue, most variously distributed, sometimes in small quantities in the protoplasm and cell-contents, sometimes filling whole cells, groups of cells, or intercellular spaces. Thus, e. g. gum, resin.

These four phenomena, that is the morphological facts which underlie them, are not the only ones, but the most important of those upon which the use of the word gland is based. It is true that those of the fourth category are distinguished as *internal* from the others as *external*. On the physiological or teleological significance of these internal glands hardly anything is known, and of the external ones but little. What is known of the latter is sufficient for drawing a real distinction between definite categories. A use of the collective name Gland in the sense used hitherto cannot therefore be justified from the physiological or teleological point of view. Still less can this be done on anatomical or morphological grounds, as is shown by what is said in this and later paragraphs. If we wish, therefore, neither to retain the word gland in this sense of an ever ready makeshift, nor to exclude it from vegetable anatomy, it only remains to limit its use to definitely characterised anatomical phenomena, and further to distinguish these in detail by special descriptions. As no one will support the first suggestion, while the exclusion of the word is obviously impossible—what would become of pili glandulosi?—we must adopt the third method. Since the parts of the epidermis, treated in this section, on the one hand unquestionably constitute the great majority of the bodies included in the term gland or glandular, and on the other hand correspond in very definite anatomical characters with one another, while they differ from other parts, the term *gland, glandular* should be applied to them, and in fact to parts of the epidermis alone, whatever may lie below them. Whatever has not those anatomical properties, should be called by a different name, which implies its position. Organs of similar structure to those in question are very rare in places other than the epidermis: still

[1] Compare De Candolle, Prodromus, II. p. 216.

[2] Flora, 1866, p. 81, Taf. II.

they do occur, as in the parenchyma of Ferns (Sect. 53). The distinction of *dermal glands* from the latter is therefore in any case necessary. It may even be retained, if it be preferred to attach to the term gland a different meaning from our present one.

The anatomical peculiarity of the glandular parts of the epidermis consists in the appearance *in the cell-wall* of that body, which is termed the *secretion* of the gland, as a part sharply defined from the cellulose layers. The wall grows in thickness at the glandular spot, by intercalation of a layer between its outer and inner side. The intercalated mass differs in material from the cellulose- and cuticular-wall, and is termed a secretion. These are the appearances directly visible. More careful investigations are necessary to answer the question as to the appearance and origin of the secretion. But in any case it is incorrect to imagine a 'perspiration' in the sense of a passage of large optically determinable masses formed in the interior of the glandular cells through the membrane. Where it is possible accurately to observe glands with resinous secretion intact, during their most intense secretion, as I can state, e. g. for the glandular hairs of Aspidium, Cistus, Pelargonium, Moluccella, Pogostemon, Primula sinensis, and also for the depressed glands of Psoralea, and for Rhododendron, there is to be found within the cell-wall clear cell-sap, and remarkably homogeneous or very uniform finely granular protoplasm, and no trace of optically visible drops of resin, the presence of which is assumed in the ordinary perspiratory theory. Hanstein's description of the visible passage of previously formed drops of resin through the cell-wall (e. g. in Viola, *l. c.*) therefore appears to me to be much in need of confirmation, in so far as it applies to glandular hairs which have not begun to wither. Existing observations rather favour the view, that the secretion—at all events the resinous secretion—is, like wax, first deposited in the wall itself, and perhaps is first formed in the wall, although it must be allowed that the material for its formation is and must be derived primarily from the protoplasm of the glandular cells, or of some other cell. In the interior of old glandular cells, in which the secretory activity has ceased, or is ceasing, larger collections of the (resinous) secretion certainly do appear. Further investigation must decide what is the cause of this phenomenon, which differs from the original and undoubtedly normal condition. According to the view derived from conditions which we have termed normal, the secretion found in the old glandular cells might have originated in the wall, and have passed from this into the interior of the cell.

Of the two main forms of glands above distinguished according to the point in the cell where the secretion is formed, the *bladder-like* glands are by far the most widely distributed; and of these again the various series of glandular *hairs*, *scales*, and *villi*. The structure characteristic of these was first clearly figured, but not understood, by Meyen (Secretionsorgane, Taf. I, Fig. 30, *d*) for the small glandular scales of Melissa officinalis. In 1854 J. Personne gave a very good description and figure of the glandular scales of the Hop (Ann. Sci. Nat. 4 Sér. I, p. 299), which for a long time were not understood: in 1856 Unger figured the structure of the glandular scales of Plectranthus fruticosus (Anat. und Physiol. p. 212), and later (Grundlinien, p. 82) the glandular villi of Cannabis: A. Weiss gave (Pflanzenhaare, *l. c.*, Figs. 258, 279 and 280, 310, 343, 364) a number of clear figures of glandular hairs, without rightly seeing the state of the case. Hanstein (Bot. Ztg. 1868, p. 697, &c.) first authenticated the characteristic structure for a large series of cases, and recently Rauter and Martinet followed him (*l. c.*, comp. p. 57). From the facts hitherto known, the general conclusion, here repeated, may be directly drawn, that the glandular or non-glandular structure is connected with no definite form or articulation of hair-structures. It should be specially asserted for hairs and villi, that capitate forms should not be identified or confused with glandular. There are glandular hairs which are not capitate (Cistus): the hairs of the 'mealy' leaves of the Chenopodiaceæ are exquisitely capitate, but not glandular, &c. It is true, however, that the majority of glandular hairs are also capitate, and that the glandular structure is localised on the head; conversely also only the minority of the capitate hairs are not glandular. A tolerably detailed review of the different forms in question cannot at present be given,

since hitherto the observers, with the exception of Hanstein, have treated the objects as exceptional, and have not thoroughly considered the points of structure in question. As examples of glandular hair-structures, which may here be described rather more in detail than above, we may begin with the bladder-like hairs, and cite once more those of Cistus creticus. The flat leaf of this shrub is grey with numerous branched hairs, and, especially at the base, with long pointed unicellular erect appressed hairs. It bears also short, multicellular hairs, which are capitate and glandular above; and lastly, numerous spindle-shaped large glandular hairs, which consist of a lower broader part composed of many disc-shaped cells, and a thin cylindrical, 1–4 celled terminal part (Fig. 36). The glandular structure occurs on the slightly widened apex, and often in places on the lateral wall of the terminal part.

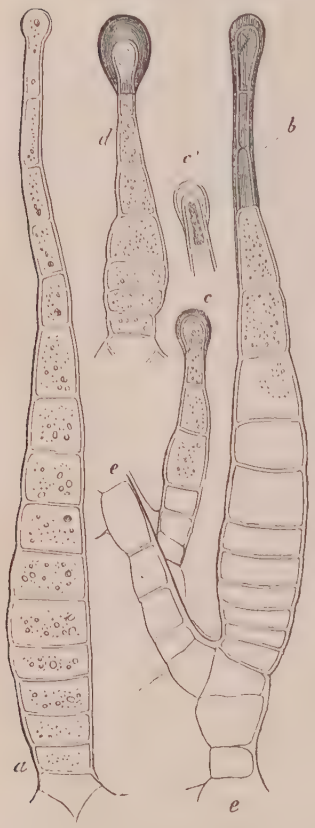

FIG. 36.—Spindle-shaped glandular hairs of Cistus creticus (375). *a* before the secretion begins, *c*, *d* with secretory bladder on the apex; in *b* the secretion extends from the apex far backwards; *c'* the apex of *c* after removal of the secretion by alcohol and ether.

Besides the examples of capitate glandular hairs and villi, and the scales connected with them already mentioned, may be named those figured by Weiss from the calyx of Maurandia semperflorens (*l. c.*, Fig. 279) and Antirrhinum majus (*l. c.*, Fig. 310), and by Hanstein from the leaf-buds of Ribes (*l. c.*, Fig. 30–33), Syringa (Fig. 68, 69), Helianthus annuus (Fig. 91, 92). The adjoining figure (Fig. 37) represents a glandular villus from the petiole of Conoclinium atropurpureum, with a non-capitate terminal portion consisting of two rows of disc-shaped cells, on which the equally high, hemispherical secretory mass, surrounded with cuticle, is seated. All the Labiatæ (comp. Meyen, Unger, Hanstein, Rauter, Martinet *l c.*) have besides various other forms of hairs, short glandular hairs, consisting of a pedicel-cell lying in the epidermis, a short stalk-cell borne by this, and seated on the latter a glandular head, covered by a great secretory bladder. The head is in the simplest cases a spherical cell; *e.g.* Pogostemon Patschouli, Fig. 38: in most cases a spherical group of four cells (Lamium album, Rauter, *l. c.*; Plectranthus fruticosus, Fig. 21, *A*, p. 59); also, it not uncommonly grows on, with further division, to a multicellular peltate scale, as in the case of the large, about 12-celled, depressed glands of many species

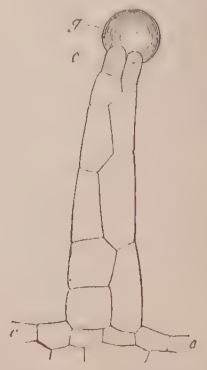

FIG. 37.—Conoclinium atropurpureum (142). From a longitudinal section through the epidermis of a young petiole. *e*—*e* epidermis, with a glandular villus; *c* terminal cell of a villus; *g* terminal cuticular bladder, filled with resin.

of Thymus (Fig. 39), Lophanthus, Satureja: also the longer stalked scales of Lavandula multifida, &c. (comp. Martinet, *l. c.*, Taf. 11). The celebrated glands of the Hop (Fig. 40, Rauter, Martinet, *l. c.*) are multicellular peltate scales, depressed in a cup-like or conical manner, and covered when mature by the bladder-like gland, which is usually raised conically, and therefore the whole appears as though it consisted of two cones with their bases in contact. As found by Meyen, the yellow glands on the foliage of Ribes nigrum closely resemble them in structure, but are always flatly disc-shaped.

FIG. 38. - Pogostemon Patschouli; young leaf, transverse section. Piece of epidermis, with a short glandular hair; secretion dissolved by alcohol (375).

On the *extended glandular surfaces*, as that of the epidermis of the branch of Betula, I have no further details to adduce. Of the sticky zones of the Sileneæ, it may be still more definitely stated that the rather difficult determination whether the secretion is formed from the peculiar prominent epidermal cells alone (Unger), or from the epidermis of the whole sticky zone, requires further investigation.

Among the *circumscribed spots*, which are usually called simply 'glands,' or compound (external) glands, two things may be distinguished from one another. First, closely

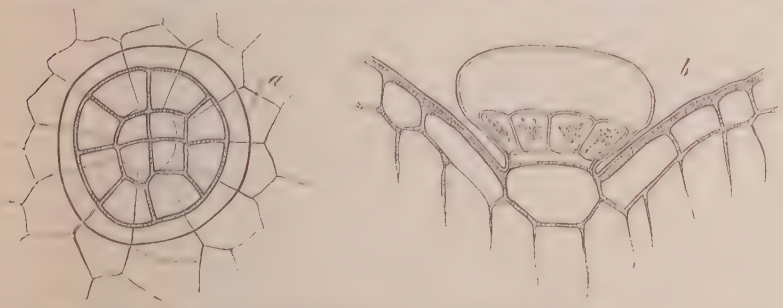

FIG. 39.—Epidermis, with glandular scales, of the upper side of the leaf of Thymus vulgaris (375). *a* surface view. *b* transverse section; secretion removed by alcohol.

circumscribed groups of glandular, capitate hairs, which are closely congregated. These constitute the round, pale or dark violet-red spot on the under surface of each stipule of certain vetches (Vicia Faba, sativa, sepium [1]), which consists in Vicia Faba of closely congregated, club-shaped, capitate hairs, of equal height, with short foot or pedicel-cell, and a head consisting of two pairs of cells one above another: glandular properties have not been observed in it in this species. The cells of the head contain strongly refractive bodies, forming dense globular aggregations or granules, together with colourless or violet cell-sap. In Vicia sativa a sugary fluid is excreted, in a manner as yet not exactly observed [2]. Further the 'glands' on the under side of the leaf of Urena sinuata are club-shaped, closely crowded, capitate hairs, which line a deeply-hollowed depression. Again, the so-called glands on the under surface of the leaf of Catalpa syringæfolia and C. Bungei [3] consist of groups of top- or fan-shaped scales with unicellular stalks, similar to the scales of Hippuris. These, as regards their structure, obviously do not belong to this category,

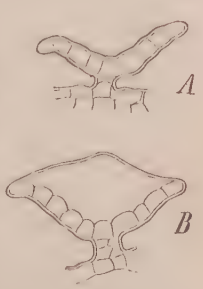

FIG. 40. — Humulus lupulus; glandular scales, transverse section (142). *A* before the secretion begins, the thick cuticle firmly attached to the surface of the cells. —*B* cuticle raised high up by the secretion, which has begun; secretion removed by alcohol.

[1] C. C. Sprengel, Entd. Geheimniss, p. 356. [2] Compare Fuckel, Flora, 1846, p. 417.
[3] Caspary, De Nectariis, p. 40.

but to others treated of above. From these must be distinguished the glandular epidermal spots, which protrude, but not in the form of hairs. A number of these have it is true the characteristic bladder-like, glandular structure of the wall, as for example the round glandular spots on the under side of the leaf, especially in the angles between the three main ribs of Clerodendron fragrans, Vent., and others, but not all species of the genus[1]; the round spots, 2–3 of which are to be found on each side of the mid-rib at the base of the under surface of the leaf of Prunus Laurocerasus[2]; the more or less depressed cup-like glands forming the end of the conical stalks or teeth on the base of the petiole of the Passifloras[3] (observed on P. atrocærulea, Hort.); the pairs of round glandular spots, which protrude at the upper end of the petiole in species of Stigmatophyllum, a genus of the Malpighiaceæ (S. cristatum, ciliatum); and the gland, the structure of which varies according to species, which lies at the upper margin of the basal part of the petiole or phyllode in the species of Acacia. The structure and form of these glandular spots have been given above for Clerodendron and Prunus. In Acacia marginata, R. Br., Calamifolia, Lindl. lophantha, they appear as convex, callus-like prominences, with a depression or furrow on the apex: their epidermis has a glandular structure above the depression or furrow, over the rest of the surface it is firm and tough-walled. In many other species (A. longifolia, latifolia, melanoxylon, subulata, longissima, obtusa, myrtifolia, striata[4]) the glandular spot lies at the base of a narrow, deep, pocket-like depression with swollen margin. In Acacia pulchella[5] the glandular hair lies on the end of a cylindrical stalk, which stands half-way between the insertions of the two main pinnæ. As already intimated, the cuticle in all these glands is raised up from the membrane by the secretion: in the flat, glandular spots of the Acacias, Clerodendron, and Laurocerasus, it is raised as a wide bladder, which often bursts in later stages of development, and in that case is often not to be found in prepared sections. The very tough cuticle of the stronger glandular spots of Clerodendron usually bursts transversely over the whole surface, with a gaping slit, which is almost visible with the naked eye. The bladder-like, glandular structure of leaf-teeth is to be found, e. g. in Mercurialis annua, Prunus, Salix, and many others[6].

Of the other numerous 'glands' which occur on leaves and leafy parts, and which were in part named above, including the numerous glandular teeth of the lamina, the peculiarly formed glandular teeth of the petiole and leaves of Viburnum opulus, V. Tinus[7], of Ricinus, and species of Cassia, and the numerous glands of the leaves of most Malpighiaceæ, &c., the structure of the surface and the secretion are not yet thoroughly investigated: but all that is known of them coincides so closely with examples which certainly belong to this category, that it is better, at least for the present, to put them in connection with these.

Intramural glands have not hitherto been described with reference to their characteristic peculiarity of structure, excepting in the above-quoted account of Hanstein. The flat, top-shaped scales of the Rhododendrons, which belong to this category (Fig. 41), are fitted into a depression of the dermal surface, and attached to short 4–5 seriate stalks. Their free outer surface is roundish and flat. They consist, according to the individuals, of 60–80 elongated cells, which form a layer, and diverge radially from the stalk. The ends of all these are directly connected with the stalk, with one another, and with the cuticle at the outer surface. 40–50 of the cells, in a ring-like series, border on the lateral periphery of the scale, and are also in immediate connection with one another, and

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[1] F. Fischer, Mém. Soc. des Naturalistes de Moscou, I. p. 246, according to Treviranus, Physiol. II. p. 35; Caspary, *l. c.*; von Schlechtendal, Botan. Zeitg. 1844, p. 6.

[2] Caspary, *l. c.*

[3] Compare Martinet, *l. c.* p. 191, figs. 238, 239.

[4] Unger, Flora, 1844, p. 703; Anat. und Physiol. p. 362.

[5] De Candolle, Prodromus, II. p. 455.

[6] Compare Reinke, *l. c.*

[7] Unger, Caspary, *l. c.*

covered by the closely applied cuticle. Their outer ends are prolonged, so that they form a radiating ring round the margin of the flat surface. The cells, about 25 in

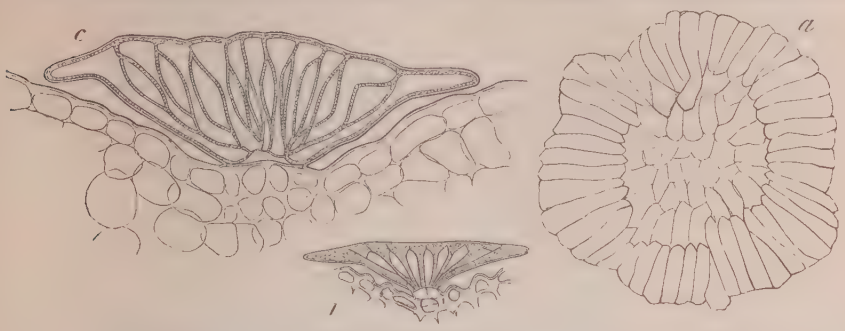

FIG. 41.—*a*, *b* Rhododendron ferrugineum; glandular scales of the under surface of the leaf. *a* surface view of a larger one; *b* transverse section of a smaller one (142). In the latter the cells are shaded; the intervening spaces filled with secretion, not shaded.—*c* Rhododendron hirsutum; glandular scales from the under surface of the leaf, transverse section (225). The cellulose membrane of the scale dotted, cell-contents and secretory space left white; over the cellulose membrane runs the cuticle, which is connected with that of the surrounding epidermis. In all cases the secretion has been removed by alcohol.

number, which form the central part of the scale, are much reduced between their two ends, and the wide interstices thus formed between their lateral cellulose walls (which turn deep blue with Schultze's solution) are filled with the secretory mixture—resin and ethereal oil.

The almost globular head of the above-named *larger* glandular hairs of the leaf of Ledum consists of 9–10 cells which diverge from the end of the stalk. The polygonal outer ends of these are distributed over the periphery of the sphere, remaining in immediate lateral connection with one another, and adhering closely to the cuticle. The cellulose walls become suddenly reduced inwards to narrow tubes, which meet at the stalk, and leave between their sides a wide space, which is also filled with a resinous secretion.

The manner in which these cavities filled with resin arise may be most clearly observed in the imbedded intra-mural glands of Psoralea (Fig. 42). At each of the clear spots on both leaf-surfaces of the above quoted species lies an almost spherical body, which protrudes into the tissue of the leaf: its outer flattened pole often lies in a slight depression or excrescence of the outer surface of the epidermis. In the superficial view of the epidermis it shows the polygonal outer walls of a group of about 20–30 cells (the number varies according to the individual), these outer walls being much smaller than those of the surrounding epidermal cells, but at least

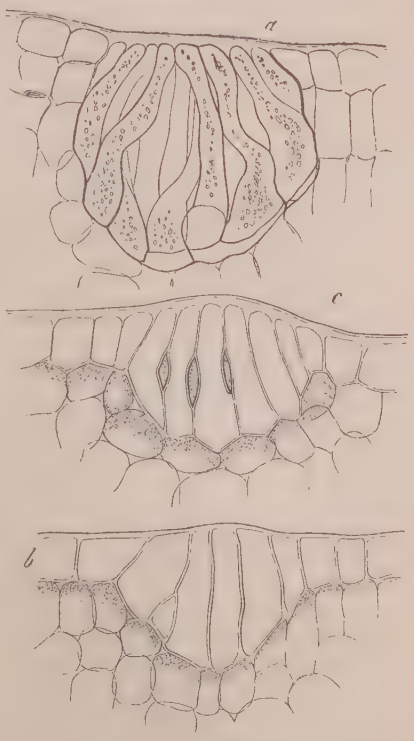

FIG. 42.—Transverse section of the lamina of Psoralea hirta; one-layered epidermis, and the tissue beneath it; the latter in *b* and *c* distinguished from the epidermis by the shading; *a* (375) an almost mature gland after removal of the secretion by alcohol; *b* (600) a very young stage of a gland, secretion not yet present; *c* (600) rather older, development of secretion beginning.

twice as thick as in these. The small polygonal outer walls belong to narrow sac-like cells, of which the peripheral ones (14 to 24 in number) run to the inner pole, curved like meridian lines. They are uninterruptedly connected laterally, thus forming with one another the wall of a hollow sphere: the 5–8 central ones are sinuous or bowed, and run through the cavity of the hollow sphere: at the inner pole they are applied with their widened ends to one another, and to the peripheral series, and thus close the hollow sphere (Fig. 42, *a*). Between the sides of the central and the inner surfaces of the peripheral cellulose walls lie wide interspaces filled with large masses of resin, or innumerable resin drops suspended in transparent fluid ('Milchsaft,' Hildebrand, *l. c.*). The contents of the sac-like cells are, when old, of a similar nature: at first they contain clear protoplasm, which is scarcely granular, and watery cell-sap.

As distinctly indicated by the mature condition, these glands originate from a single primary epidermal cell, which bulges inwards, and is repeatedly divided by walls perpendicular to the surface. The segments elongate in the same direction: their lateral cellulose walls are at first uninterruptedly connected (*b*, Fig. 42). During the elongation resin appears at the limiting surface, at first as an homogeneous narrow and short intramural layer, at the middle of the cells, forming transverse rings round the central ones (*c*, Fig. 42): gradually it increases in height and thickness, till it attains the size of the large interstices above described. At first, and during the most active growth of the resinous layers, the cells contain a very thin transparent protoplasmic lining, and quite clear colourless cell-sap.

The *secretion* of the dermal glands of all categories is in most cases resin, or a mixture of resin and ethereal oil: *e.g.* Betula, Humulus, Labiatæ, Primula, &c. A complete enumeration of the chemical relations of these bodies cannot be undertaken here. In other cases it consists of bodies which swell and dissolve readily in water (vegetable mucilage, gum), as for instance in the buds of the Polygonums (Hanstein, *l. c.*); or of mixtures of these and resin, as, according to Hanstein, in most leaf-buds, *e.g.* Cunonia, Viola. More rarely, on parts which do not belong to the flower, it consists of mixtures of gum and sugar: thus in Viburnum Tinus, Clerodendron fragrans, where the sugar may even crystallise, Prunus Laurocerasus, Acacia, &c. (Von Schlechtendal, Caspary, Unger, *l. c.*). The resinous secretions may be rather solid, *e.g.* Aspidium; but certainly in the majority of cases they are soft and sticky: those which swell and dissolve easily in water are normally always very watery; most secretions are therefore naturally moist and sticky. The character of the surface is not influenced when the moist secretion remains in the glands, and when only its volatile constituents evaporate through the membrane. This is the case in all intramural glands, and those with tough resistent cuticle, as in Humulus and most Labiatæ.

In the bladder-like glands with delicate cuticle the latter is either burst by internal causes, *e.g.* by increasing aggregation of the secretion, as in the sugar glands of Clerodendron, Acacia marginata, the glands of many leaf-buds; or rupture of the cuticle results readily from external lesion, and the surface thus becomes sticky through the escape of the secretion. On hair-structures of mature parts the secretion soon ceases after rupture of the cuticle, and the glandular cells dry up: fresh secretion may in that case proceed from other later-developed glandular hairs. In the glandular spots, which lie over the ends of the vascular bundles, the secretion appears in many cases, at all events, to continue long after the rupture of the cuticle; still we must in these cases distinguish more exactly how much of that which is excreted is due to secretion itself, and how much to water which filters from the vascular bundles. In unfolded foliage-buds, according to Hanstein, the rupture of the cuticle is often followed by its renewal and the formation of new secretory layers.

Like hair-structures generally, the glandular hairs are also in many cases transitory organs, which are present in the bud, but disappear after the bud unfolds. The glandular epidermis of many leaf-teeth also secretes while in the bud, and afterwards

dies off[1]. Hanstein has termed these organs which cover the buds with a sticky secretion 'Beleimer,' or Colleters, and their sticky product bud-glue, or Blasto-colla.

There is as yet only one case known to me in which such mucilage, covering buds, has an origin other than that indicated. The bases of the young leaves of Osmunda[2] are covered with a rich amorphous mucilage. This originates from long septate hairs, with large bead-like cells, each of which, in the stages of development observed, is completely filled with a mass of mucilage. The origin of the latter remains to be investigated. On treating with water, the mucilage swells and escapes as an amorphous hyaline mass from the burst cellulose membrane.

Sect. 20. The capitate hairs with mealy dust—*pili pulverulenti*—should at present, for the sake of consistency, be separated from the glandular hairs, but they must be treated in immediate relation to them. To these hairs the under-surfaces of the leaves of the so-called gold and silver ferns owe their dusty covering, which is white (Gymnogramme tartarea, calomelanos and other species, Notholaena nivea, Cheilanthes spec.) or golden yellow (Gymnogramme sulfurea. Martensii, &c., Pteris aurata), while on the foliage of the mealy Primulas it appears light yellow (Pr. marginata) or usually white (Pr. Auricula, farinosa, &c.).

The mealy covering of these plants is not excreted like the wax coverings, by the whole epidermis, but exclusively by the globular apical cells of small hairs, which are borne on a short unicellular (Gymnogramme) or two-celled (Primula) stalk (Fig. 43)[3]. It appears on the whole surface of the apical cell in the form of rods or small needle-shaped crystals. In Gymnogramme these radiate from the whole surface of the apical cell; their length may greatly exceed the diameter of the latter. In the Primulas they are irregularly aggregated. In not quite intact specimens, especially of the Primulas, they are often shattered to heaps of small fragments, and scattered over the whole epidermis. The covering consists of resinous bodies[4], which are to a great extent easily soluble in cold alcohol. In Gymnogramme I found, after solution in alcohol, a finely granular residue, which dissolved in ether. Klotzsch[5] names the bodies in question Pseudo-stearoptene: they are, according to his statement, which certainly requires revision, easily crystallised out from the alcoholic solution (I obtained only aggregates of very small crystals): the crystals are rather hard, heavier than water, fusible at 50°, sublimated without change when air is excluded, slightly aromatic, soluble in warm water (?!), alcohol, ether, acetic acid, and alkalies.

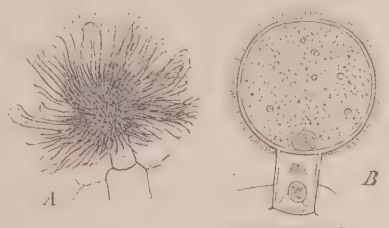

Fig. 43.—Gymnogramme tartarea. *A* (142) dusty hair from the under surface of the leaf, floating on water; the round apical cell covered by the erect radiating rods of resin.—*B* (375) a similar hair after momentary action of cold alcohol; the rods are for the most part dissolved; in their place remains a finely granular layer, which is quickly dissolved in ether. In the apical and stalk cells are nuclei; the larger granules in the apical cell are chlorophyll grains.

On the foliage of many plants closely allied to those in question—Filices, Primula sinensis, &c.—instead of the dusty hairs, there are found typical resin-secreting,

[1] See Reinke, *l.c.*

[2] S. Milde, Monogr. Generis Osmundæ, Vindob. 1868.

[3] Link, Icones Selectæ, Heft IV. Tab. III. figs. 7–9.—Mettenius, Filices horti Lipsiensis, p. 42.

[4] Göppert, N. Acta Acad. Leopold. Carol. XVIII. Suppl. I. p. 206.

[5] Monatsber. d. Berlin. Acad. 1851, Dec. Botan. Zeitg. 1852, p. 200.

bladder-like glandular hairs. This fact, besides the other points of agreement, shows how nearly the two structures are allied. In Gymnogramme I always found the crystalline covering seated only on the smooth cuticle of the apical cell. On young, as yet unfolded, fresh leaves of Auriculas, the apical cell of the hair has often a typical bladder-like glandular structure: so that the cuticle which surrounds the resinous secretion is extremely thin, and the apical cell bears occasionally one large resin-bladder, usually two or several small ones. On older leaves I did not observe these bladders: those which occur on young leaves are replaced after long immersion in water by the above-described crystals. All these phenomena, which require more careful observation, point again to the fact that we have here to deal with a peculiar form of glandular hair and glandular secretion.

Sect. 21. Darwin, in his 'Insectivorous Plants,' has drawn attention to organs belonging to the epidermis, which in their structure and development are closely allied to the hair structures and dermal glands above described, but are distinguished by the fact that, at least in the closely-observed cases, when subjected to continued chemical or mechanical stimulus, they secrete at their surface a fluid, which holds in solution a free (organic) acid, and a ferment similar in its action to Pepsin. As the result of the interaction of the two dissolved bodies, they are capable of dissolving and digesting albuminoid substances, and the solution of these, as well as of Phosphates, salts of ammonia, &c., is absorbed by them or—a point which cannot be considered as generally established—by the surrounding tissue. According to this digestive function these organs may be termed *Digestive glands*. Besides the above solutions there often occurs a rich excretion of mucilage which is sticky, and swells with water, especially in species of Drosera, Drosophyllum, and Pinguicula. This appears in the plants named even independently of stimulus, but in this case the acid reaction and digestive effect are absent. In others the mucilage is not observed.

The organs in question, and the power conferred by them of digesting animal substance and absorbing it as nourishment, are at present known in the case of the peculiarly-formed leaves of Droseraceæ, especially species of Drosera, Drosophyllum, Dionæa, and species of Pinguicula. Other plants also absorb dissolved animal bodies as nourishment by means of their leaves. This is certain in the case of Utricularia, and very probable in that of Aldrovanda, Nepenthes, Sarracenia, &c. They then show corresponding organs, which are probably to be regarded as digestive glands, though they are not at present certainly understood.

The undoubted or presumptive digestive glands have (when they belong to the epidermis) the position and cellular arrangement either of circumscribed dermal glandular spots, or of hairs or scales.

They are either situated above the ends of vascular bundles (Drosera, and sometimes in Nepenthes) or have no direct relation to these (e. g. Pinguicula, Dionæa).

Of the allied hair structures, which rise above the epidermal surface, those delicate, long-stalked, umbrella-like scales (p. 64) which are found in large numbers on the leaf-surface of the Pinguiculas have already been mentioned. They secrete on their upper surface. The digestive glands on the upper surface of the leaf of Dionæa[1] and Aldrovanda are quite short, umbrella-like, stalked, round, multicellular scales,

[1] [C. de Candolle, *Ref.* Bot. Jahresber. 1876, p. 383, Oct.]

without any specially remarkable arrangement of the cells. In the Utricularias the digestive function may be carried on by the four-armed hairs already mentioned (p. 62), which are seated in large numbers on the inner surface of the sacs which catch animals. In the investigated species of Drosera, and in Drosophyllum, the form and arrangement of the cells on the secreting leaf-teeth is exactly like those of the circumscribed dermal-glandular spots, occurring especially on the teeth of the foliage-leaves. The description of them for Drosera will be better given below (Chap. VIII) in connection with that of the endings of vascular bundles.

The presumptive digestive glands of Nepenthes[1] so often investigated, but lately very thoroughly treated of by Wunschmann, have the most peculiar arrangement. They are situated in these plants on the middle and lower portion of the pitcher-shaped part of the leaf, on the inner surface, in many species also on the inner surface of the lid. They belong to and arise from the epidermis, and consist of a disc-shaped basal portion, formed of one small cubical cell: this bears a rounded head, composed of prismatic thin-walled cells, arranged in a perpendicular, radiate manner. Their whole form is thus that of a globular wart. Each of these very numerous warts, which can even be recognised with the naked eye, lies in the pitcher in a pouch opening into it: the pouch is formed by extension of the row of epidermal cells surrounding the upper margin of the wart in the form of a semicircular sharp-edged band, which is drawn forward as a cap over the wart. On the lid of the pitcher this band is equally high all round. In the upper part of the pitcher the glands are absent from the inner surface: the epidermis is here covered with granules of wax in a simple layer, and is smooth, excepting that numerous small semilunar hair-cells (concave on the under side) are inserted between the slightly undulating epidermal cells. On Sarracenia, compare p. 69.

With all the similarity of structure of the digestive organs in question to that of the above-described dermal glands, they differ in structure fundamentally from these in this point, that their secretion—and also, as far as investigation extends, the mucilage of Drosera and Pinguicula—does not appear in the wall, between the cellulose wall and cuticle, but on the free outer surface of the latter.

Other generally remarkable, anatomical peculiarities cannot at present be brought forward, without far transgressing the boundaries here imposed, and entering deeply into physiological details. Here therefore, after this short notice, we can only refer to the recent literature on insectivorous plants, and a few older works on the anatomy of the glands in question, some of which have been already cited.

Ch. Darwin, Insectivorous Plants, London, 1875.—J. D. Hooker, Address to the Dep. of Zoology and Botany of the Brit. Association, Belfast, 1874.—F. Cohn, Ueber die Blasen von Aldrovanda und Utricularia, Beit. z. Biologie, Heft III. p. 71.—Treviranus, Meyen, Oudemans, Wunschmann, *l. c.*, Schacht, *l. c.*, Utricularia, comp. p. 62.—E. Morren, Note sur le Drosera binata, Bull. Acad. Belg. 1875.—Aldrovanda, Cohn, Flora, 1850.—Caspary, Bot. Ztg. 1859, p. 117, &c.—Fraustadt, Anatomie d. Dionæa muscipula, in Cohn, Beitr. z. Biol. d. Pfl. Bd. II. p. 27.—Fr. Darwin, The process of aggregation in the tentacles of Drosera rotundifolia, Micr. Journ. vol. XVI. N.S.—Warming, in Videnskab. Meddelelser fra nat. Forening i Kjöbenhavn, 1872, p. 168, (French Résumé, p. 18; Drosera).

[1] Treviranus, Zeitschr. f. Physiologie, III. p. 73.—Meyen, Secretionsorgane.—Oudemans, De Bekerplanten, Album d. Natuur, Groningen, 1863 and 1864.—Wunschmann, Ueber d. Gattung Nepenthes, Diss. Berlin, 1872.

Sect. 22. Of generally distributed, incombustible constituents of the membrane, compounds of Silicon, Calcium oxalate and carbonate are often contained in the epidermis in remarkable quantity and form.

Presence of silica, or *silicification*, is observed specially in epidermal layers, and is particularly abundant in the cuticularised outer walls. Highly silicified epidermal layers are characterised by hardness and firmness. Equisetum hiemale, Calamus spec., Gramina, leaves of Ficus sycomorus, F. trachyphylla, Deutzia scabra, Celtis, Ulmus, Davilla brasiliana, Parinarium senegalense, Magnolia grandiflora: a definite relation however does not exist between silicification and hardness: the hard epidermis of the leaves in most Palms, Mahonia aquifolium, Drimys Winteri, Rhododendron, Hakea spec., Phormium tenax, the phylloclades of Ruscus aculeatus, and in Cycas revoluta, has no silica. (Mohl.)

Calcium oxalate is observed in the form of granules, or obvious crystals, in the epidermis, especially in the cuticular-layers in the leaves of Welwitschia, of many Cupressineæ, and Taxineæ, in species of Ephedra, the leaves of Dracæna reflexa, arborea, Draco, umbraculifera, Sempervivum calcareum Jord., and species of Mesembryanthemum. When it occurs in large quantity it often gives to the epidermis a dull white colouring, as in the above-mentioned Sempervivum, Mesembryanthemum lacerum, incurvum, stramineum, Lehmanni, vulpinum, &c., and the white spots of the leaves of M. tigrinum.

Calcium carbonate is contained in great quantity in the membrane of many hairs, and especially in the peculiar peg-shaped wall-thickenings known under the name of *Cystoliths*, especially in the Urticaceæ and Acanthaceæ.

Silicon-containing epidermal layers have, according to Von Mohl's widely extended investigations, been observed in species from 41 families of the most various large divisions of the vegetable kingdom.

The silica is found chiefly in the outer layers of the external wall: but Von Mohl notes[1] that he had not observed it to be restricted to the outer cuticular lamella alone. In most cases, when the epidermis is smooth and flat, the silicification extends over the whole outer wall and the outer part of the lateral wall of the epidermal cells: *e.g.* in many grasses and Cyperaceæ. More rarely, and only where the silicification is extreme, the inner wall of the epidermal cells, and the sub-epidermal cells, which border laterally on the respiratory cavity (Deutzia scabra), take part in it. The guard-cells of the stomata are silicified all round or partially.

Partial silicification of the cell-wall occurs in other solitary cases: thus it is limited to the protruding knobs in the median line of the epidermal cells in the stem of Scirpus palustris and mucronatus. On the subsidiary cells of Equisetum hiemale the transverse bands on the lower wall are only silicified in their inner part which borders on the slit, not in their outer part (Fig. 24, p. 72, *A*, *C*). Further there belong to this category the stalks of the cystoliths in the Urticaceæ, the silicification of which was proved by Payen, and cystolith-like outgrowth of the wall of the above-named Borragineæ and Compositæ (Onosma, Cerinthe, Helianthus trachelifolius, comp. p. 106). On the stinging hairs of Urtica dioica the upper brittle part of the wall is very strongly silicified, the lower part but little (Mohl, *l. c.*, 219).

Very often there are varieties in the silicification of cells and groups of cells of one epidermal surface, due to the unequal extent of the silicification in closely neighbouring

[1] Von Mohl, Botan. Zeitg. 1861, pp. 209, 305, where also the literature on the subject is thoroughly treated of; and Hofmeister, Die Lehre von der Pflanzenzelle, p. 242.

parts, or one part is strongly silicified, another not at all. In the epidermis of many grasses, the upper of the short epidermal cells, which are arranged in pairs one above another, are distinguished from the rest by specially strong silicification of their wall, the others are more slightly silicified, and in many cases not at all (Internodes of Saccharum officinarum). Often the hairs are centres of silicification. They alone may be silicified (leaf of Campanula cervicaria, Ficus Joannis Boiss., Urtica excelsa, lusitanica, dioica); or the process begins in them, and extends around the base of each hair centrifugally over the epidermal surface, and spreads evenly or unevenly over it. In the latter case, even in the mature organ, each hair is seated in the centre of a disc consisting of silicified epidermal cells, which usually turns white after death. This is separated from other similar discs by interspaces with weaker silicification (*e.g.* leaf of Humulus, Ulmus campestris, Tectona grandis and other Verbenaceæ, Cucurbitaceæ, Pulmonaria saccharata, Cerinthe major, Silphium connatum, Helianthus grosseserratus, many Dilleniaceæ, Chrysobalaneæ, &c.), or by interspaces without silicification (leaf of Cerinthe aspera, minor, Onosma stellulatum, arenarium, Lithospermum officinale, Helianthus tuberosus, trachelifolius, &c.) Often (*e.g.* Ulmus campestris) the cell which is the centre of silicification does not grow out to a hair.

In many leaves, especially of Dicotyledonous plants (*e.g.* Humulus, Morus alba), the epidermis of the upper side is much more strongly silicified than that of the lower: in the latter the silicification appears often to be absent, while it is present in the former (*e.g.* Helianthus trachelifolius, Heliopsis lævis, Obeliscaria columnaris). In all these phenomena it is impossible to ignore a certain analogy with the cuticularisation of membranes.

On the intramural deposition of *Calcium oxalate*, comp. H. Graf zu Solms-Laubach, Bot. Ztg. 1871; Pfitzer, in Flora, 1872, p. 97.

The most remarkable points of deposition of *Calcium carbonate* in the epidermis are those thickenings of the walls termed by Weddell[1] *Cystoliths*.

The Cystoliths of the Urticaceæ were discovered by Meyen in Ficus elastica: he described them thoroughly in 1839[2]: later they, as well as those of allied plants, were investigated by Payen[3], Schacht[4], and Weddell (*l. c.*). Schleiden[5] contributed some observations on them, and brought forward a view of their morphological significance, which, like some statements of Payen on their structure, have been corrected by investigations recently conducted[6].

On the still folded leaf of Ficus elastica (Fig. 44), surrounded by its stipular sheath, the epidermis of the upper side consists, long before the unfolding, of a single layer of elongated prismatic cells with their longer axis perpendicular to the surface of the leaf (*A*). These are mostly of equal size and similar shape. They are together covered by the cuticle, and are mostly provided, below this, with a massive cellulose outer wall, which exceeds the lateral walls in thickness. Single cells of this layer now thicken their outer walls four to six or more times as strongly as the rest. The latter then divide by longitudinal and transverse walls, to form the four-layered epidermis. The cells with strongly thickened outer walls remain undivided, their outer wall grows only very little further in the direction of the surface of the leaf, so that it soon appears as a rather stronger band of membrane between laterally adjoining and thickening cell-

[1] Ann. Sci. Nat. 4 sér. II. p. 267. [2] Müller's Archiv, 1839, p. 257.
[3] Memoires sur le développement des végétaux. Mém. présentés de l'Acad. des Sciences, tom. IX.
[4] Abhandl. der Senckenbergischen Gesellsch. I. p. 133. [5] Grundzüge, 3 Aufl. p. 341.
[6] [See also Penzig, Verbreitung d. Cystolithen, Bot. Contralbl. Bd. 8. 1881, p. 393.]

walls. The other part of these cells however becomes expanded to form a great oval bladder which intrudes deeply into the sub-epidermal parenchyma. As soon as the processes of expansion and division in the neighbouring cells begin, there grows from the middle of the thickened outer wall, perpendicularly into the interior, a peg-shaped process (consisting of cellulose), the blunt end of which swells into a knob (*B*). When the leaf is fully developed (*E*) the swelling has the form of an egg-shaped or almost spherical body, which attains a size filling half or more than half of the cell. This is the cystolith, which is thickly covered on its exterior with pointed and blunt radially diverging conical warts, and is suspended in the cavity of the bladder-like cell by an irregularly cylindrical stalk, which is continuous directly into the original thickened outer wall. The whole body is impregnated with calcium carbonate, and

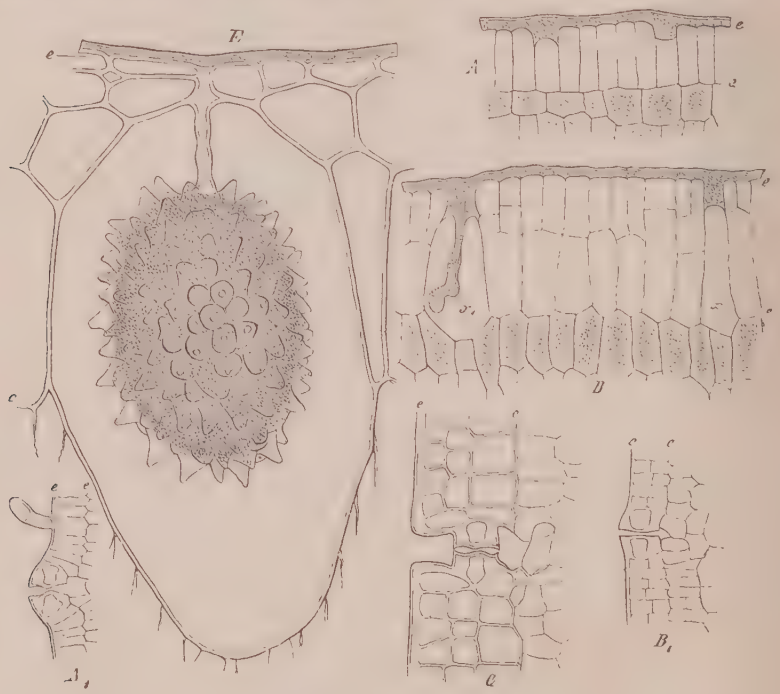

FIG. 44.—Ficus elastica; leaf, transverse section. *e—e* in each case the thickness of the epidermis; *A* (600) upper side; A_1 (390) under side of the same very young leaf; in A_1 an already complete stoma, which remains superficial, and a hair (transient); in *A* two cystolith-cells, recognisable by their thickened outer wall, epidermal cells as yet undivided.—*B* (600) upper, B_1 (390) under side of a rather older leaf, epidermal cells undergoing division. In *B*, *x* is a younger and x_1 an older stage of a cystolith, already showing the peg-like excrescence of the wall.—*C* (390) older leaf, under side; division of the now three-layered epidermis is complete, stoma depressed, but the definitive size and form of the parts is not yet attained.—*E* upper side of a mature leaf, four-layered epidermis, cystolith-cell (375).

the stalk also with silica: it has a homogeneous glassy appearance, and in the pointed warts there is often stratification and granulation. Acids dissolve the calcium salt, bubbles of carbonic acid being produced. After solution the stalked body remains behind with its original attachment; the stalk is but little altered, the swelling remaining as a delicate cellulose skeleton, the outline having become more irregular: the interior shows well-marked stratification and delicate radial striation, the layers from the end of the stalk onwards being nearly concentric with the surface.

The epidermis of the under side of the leaf of Ficus elastica has similar, but smaller and more scattered cystoliths. The same structures have been proved to exist in all other species of Ficus which have been investigated on this point, the form and size varying according to the species. The cystolith-cell has in other species a much broader outer wall at the surface of the epidermis than that in Ficus elastica (e. g. F. australis, salicifolia), or its thick outer wall itself rises as a more or less long hair-like apex above the latter (Ficus Carica, montana, ulmifolia).

Other Urticaceæ have similar cystolith-cells, and cystoliths in the epidermis: species of Parietaria, Boehmeria, Forskâhlia tenacissima, Celtis, Morus, Broussonnetia, Humulus, Cannabis, Conocephalus, Urtica (Payen). A form differing from the round or oval is shown by the bodies in question in Pilea decora, densiflora? (Weddell), Urtica macrophylla (Fig. 45). The cystolith is here spindle-shaped, straight or with two curved legs (Pilea densiflora?), it lies in a cell of form similar to itself, of which the greatest diameter is parallel to the epidermal surface, and it is attached to the middle of the outer wall of the cell by a stalk, which arises from the middle of one side of it. The structure of the spindle-shaped cystoliths is the same as that of the round ones. In the Urticaceæ the cystoliths are absent in Ulmus and Dorstenia (Payen).

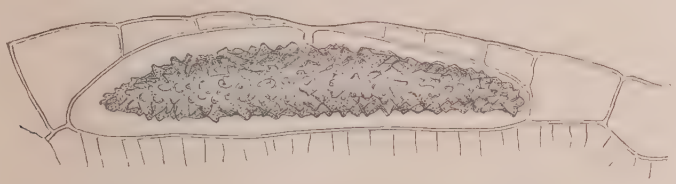

FIG. 45.—Urtica macrophylla; piece of the epidermis with cystolith-cells, from the upper side of the leaf; transverse section (225).

The cystoliths of the Acanthaceæ, which were first found by Gottsche (in Schacht, *l. c.*), resemble in structure those of the Urticaceæ: their form is seldom round (Justicia carnea, Schacht), usually spindle-shaped, or like a transversely halved spindle. Their attachment by a stalk is also often similar to that above described (Justicia carnea, Beloperone oblongata, Schacht, *l. c.*): but the half-spindle-shaped ones are attached by a very thin short stalk, arising at a point of their truncated end, to a lateral wall of the cell which conceals them. Schacht describes cystoliths in the epidermis of the above Acanthaceæ, further of Barleria alba, Ruellia formosa, livida, Justicia paniculata, to which Eranthemum pulchellum, Goldfussia anisophylla, and others should be added. He failed however in finding them in Justicia purpurascens and Acanthus mollis.

On the occurrence of cystoliths in the sub-epidermal tissue in Urticaceæ and Acanthaceæ, see sect. 32.

'The knobs which surround the base of the hairs in the Borraginaceæ, and many Synantheræ[1], are allied to the cystoliths of the nettle-like plants.' The base of these hairs, which is embedded in the epidermis, is surrounded by one or two concentric ring-shaped rows of cells which are distinguished by their wall, on the whole surface facing the hair, being covered with a well-marked stratified thickening, which protrudes inwards

[1] Von Mohl, Botan. Zeitg. 1861, p. 229.

in the shape of knobs. This fills one-half, two-thirds, or often almost the whole of the cell-cavity. This thickening of the membrane contains (besides a compound of Silicon) a large quantity of calcium carbonate, partly as a homogeneous infiltrated mass, partly in the form of very small granules, or often of splitting crystalline masses. Examples, Cerinthe aspera, major, minor, Onosma stellulatum, arenarium, Echium vulgare, fruticosum, Lithospermum officinale, Anchusa italica, Helianthus tuberosus, trachelifolius, macrophyllus W., Obeliscaria columnaris, Heliopsis lævis[1]. In the multicellular hairs of Helianthus similar thickenings often occur in the lowest cell, both laterally and on the under surface of the upper wall. Whether the silica-containing rosettes of cells in Ulmus, Dilleniaceæ, and Chrysobalaneæ (Von Mohl, *l.c.*) which surround the hairs or rudiments of hairs, and resemble the above, also contain calcium carbonate, is not stated.

In the hairs of many *Cruciferæ*—Alyssum, Cheiranthus Cheiri, Capsella, &c.—the presence of calcium carbonate in very large quantity is shown by reagents. It does not occur as single distinguishable particles, but is contained mainly (or wholly?) in the outer layers of the membrane, especially in the wart-like thickenings which protrude outwards (comp. Fig. 21, *D*, p. 59). These appear on the fresh hair mounted in water as strongly refractive, blueish and bright, after solution of the lime-salt very pale and transparent.

Also other strong hairs (Borragineæ, Helianthus) appear to contain large quantities of calcium carbonate in their lateral walls.

Sect. 23. **Incrustations of Lime.** Calcium carbonate is often found in finely granular masses, deposited, as an incrustation, upon the outer surface of the cuticle.

(1) On the epidermis above the ends of the vascular bundles of many land plants. On these spots lies a white granular scale of lime. This is the case in many Fern leaves: Polypodium subauriculatum, meniscifolium, repens, aureum, sporadocarpum, areolatum, crassifolium, morbillosum, &c., species of Nephrolepis, Aspidium leucostictum, albopunctatum, pedatum, Lomaria attenuata[2], and on the leaves of the white incrusted species of Saxifraga[3]. The above-named Ferns show at definite points on the upper surface of the leaf shallow, in Lomaria attenuata deep, flask-shaped depressions, in which, when the definitive development of the leaf is attained, there appears the white scale of lime, which is not renewed after removal. Also in the Saxifrages the lime scales are excreted in depressions, which lie on the upper side of the leaf—in the species of Euaizonia on each of the marginal teeth, which are covered with short blunt hairs—in S. cæsia, 4–6, in pairs on the two margins, and a single one at the end of the middle nerve: in S. retusa and oppositifolia 1–3–5 on the upper side. The depressions are filled up with the mass of lime: their epidermis is distinguished from that of the rest of the leaf-surface by the small size and thin walls of the cells rich in granular protoplasm, which in Lomaria attenuata grow out as papillæ. Stomata are absent in the depressions in the above Ferns (Mettenius), in the Saxifrages the water-stomata described p. 53 are always present.

(2) On the leaves and herbaceous stalks of Plumbagineæ[4] (species of Plumbago,

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[1] Compare von Mohl, *l.c.* p. 227.

[2] Treviranus, Verm. Schriften, IV. p. 66.—Mettenius, Filices horti Lipsiensis, pp. 8, 9.

[3] Unger, Einfluss. des Bodens, &c., p. 178.—The same, Beitr. z. Physiol. d. Pfl. VIII.—Sitzungsbr. d. Wiener Acad. Bd. 43. p. 519.—Mettenius, *l.c.*

[4] Braconnot, Ann. Chim. et Phys. LXIII. p. 375.—Treviranus, Physiol. II. p. 101.—Mettenius, *l.c.* p. 9.

Statice, Armeria) occur numerous lime-scales scattered over the surface without any direct relation to the ends of the vascular bundles. Each of these appears on the outer face of a small group of cells of peculiar form, and exactly similar groups of cells occur in species in which no excretion of lime occurs, as Armeria vulgaris, plantaginea, Statice scoparia, latifolia, purpurascens, alata (Mettenius). They consist of eight cells, arising from one epidermal cell which appears in surface view rounded and quadratic. This is divided by two walls, perpendicular to the surface and to one another, into four: each of the latter again divides by a perpendicular wall into two: one very small one forming the inner angle, and one being peripheral. The cells of these groups are thin-walled, and contain dense finely granular protoplasm. Their outer walls lie in many species at the surface: in others, especially thick-skinned species, they form the base of hollow depressions, e. g. Statice alata, purpurea, monopetala.

(3) In water-plants, especially submerged ones, the whole epidermal surface is often equally covered with a thick layer of calcium carbonate. Reinsch[1] found the lime-covering on the upper side of the swimming leaves of Potamogeton natans continuous over each stoma during the active vegetation of the leaf. In many land-plants also, which form lime-scales,- -Saxifrages, e.g. S. crustata, Statice spec.—the whole epidermis is covered with a thin crust of lime.

The origin of the lime-coverings remains to be investigated. We may almost imagine in the case quoted under (3) a precipitate having been formed by the removal of carbonic acid from the lime-containing water, and explain the lime-scales over the ends of the vascular bundles by the evaporation of drops of lime-containing water, especially since the exit of such drops on the young leaf in the Ferns and Saxifrages really takes place: and we may explain the incrustation which occurs near the scales as arising from partial solution of the scales in water containing carbonic acid, and subsequent repetition of the evaporation. These are plausible explanations, for which however the proof is wanting: for the excretion of lime in the Plumbagineæ it is not admissible.

Analyses of the lime-coverings showed in Potamogeton, besides calcium carbonate, traces of Silicic acid and oxide of iron (Reinsch), in Saxifraga crustata (Unger *l. c.*) to 4·146 parts calc. carb. 0·817 of carb. of magnesium.

The scales of the Ferns, Saxifrages, and Plumbagineæ leave behind a colourless gelatinous residue when the lime is dissolved with nitric acid.

Incrustations of carbonates of alkalies are described in the case of the foliage of species of Tamarix, Réaumaria, shore-plants. Notices on this: de Candolle, Physiol. p. 237; Treviranus, Physiol. Vol. II. p. 101; Unger, Anat. und Physiol. p. 369. Definite investigations do not exist.

[1] Flora, 1858, p. 723.

SECTION II.

CORK.

Sect. 24. **Cork**[1] is formed in the mature plant as a tissue having the fundamental physical properties of cuticularised epidermis, the place of which it supplies when the latter is thrown off in the normal course of development (comp. Chap. XV), or where the living parenchyma is laid bare by wounding, or where it is to be isolated from the effects of injuries which have penetrated to the interior. Rarely, as in many bud-scales, cork appears simultaneously as a strengthening of persistent epidermis.

All investigated phanerogamic land-plants are capable of forming cork. In the Cryptogams it is only found in isolated cases, namely on the surface of the Rhizome of the Ophioglosseæ[2].

Cork-formation always originates in the epidermis or in living parenchymatous cells, and indeed in the latter without distinction, to whatever member or region they may belong. Wound-surfaces, of whatever sort, are closed and healed by it; and diseased or dead parts are isolated from those still living. In the normal course of development (disregarding the surfaces of separation of members thrown off, which are here to be placed in the category of wound-surfaces) it appears especially on the surface of such parts as the stems and roots of most Dicotyledons, Gymnosperms, and a few Monocotyledons, which have a long-continued and abundant growth in thickness, not continuously followed by the successive peripheral layers of tissue (Chap. XV); it is less generally present on the surface of long-lived, firm, but not continuously thickening stems and roots of Monocotyledons. Most of the latter retain their epidermis, but it is replaced by cork in the stem and the roots of Pandaneæ, epiphytic Aroideæ (Philodendron, Monstera, Anthurium, Tornelia[3]), the roots and rhizomes of Dracaeneæ, Strelitzia, Dioscorea, Zingiberaceæ. Finally, in rare cases, formation of cork occurs normally on the surface of leaves[4], as on the scales of the winter buds of many dicotyledonous and coniferous trees, Aesculus Hippocastanum[5], Ulmus montana, Populus, Carpinus, Corylus, Abies excelsa[6].

The cork-formation begins in a single layer of cells parallel to the surface which is to be shut off, by the occurrence of divisions also parallel to that surface. This layer of cells, which relatively to the cork-formation may be called the *initial* layer, is the epidermis itself in certain cases of normal development of Dicotyledons, to be more accurately treated of below (Chap. XV); in all other cases it is a

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[1] Sanio, in Pringsheim's Jahrb. II. p. 39. Further literature in Chapter XV. [See also F. von Höhnel, 'Ueber den Kork und verkorkte Gewehe überhaupt,' Kaiserl. Akad. d. Wiss. in Wien. Nov. 1877.]

[2] Russow, Vergl. Unters. p. 121.

[3] Von Tieghem, Str. d. Aroidées, *l.c.*

[4] [Compare Bachmann, über Korkwucherungen auf Blättern, Pringsheim's Jahrb. XII. p. 191.]

[5] Hanstein, Botan. Zeitg. 1868, p. 721.

[6] Areschoug, Om den inre byggnaden i de trädartade växternes Knoppfjäll. Lunds Univ. Arsskrift, tom. VII (1870).

layer of parenchyma lying immediately below this or deeper. In the healing of wounds it is as a rule that layer of parenchyma which lies immediately within that injured by the wound: still there occur exceptions to this rule, as a more deeply-seated layer may become the initial layer of the cork. The forms respectively of the initial cells, and of the layer of cork which results from their division, depend therefore upon that of the surface to be shut off. In wounds it may have all possible shapes; in normal cork formation it resembles the normal surface of the member.

By the divisions parallel to the surface the single layer of initial cells is converted into a multi-seriate meristematic zone. Of the layers of this zone the outer, i.e. those opposite the normal surface, or the wound surface, assume at once the properties of cork-cells and accordingly lose the power of division. But a single layer of cells bordering the cork-cells internally retains as a rule the properties of meristem, and therewith the power of continuous division: this is the cork-forming or *phellogenetic* meristem, or the phellogenetic layer.

On parts still increasing in girth, the layer of phellogen follows this growth, and by divisions perpendicular to the surface can increase the number of its cells, and of the layers of cork produced from them.

From what has been said it follows that the cells of a mass of cork are arranged in rows perpendicular to the surface, each of which corresponds to one initial cell. As the cork-covered surface increases in circumference each series may successively be doubled. The serial arrangement of the elements of the cork perpendicular to the surface is always very regularly preserved. The walls parallel to the surface usually correspond pretty closely in neighbouring series one to another, so that besides the arrangement in perpendicular series there is also a no less regular arrangement in layers parallel to the surface.

The succession of the divisions parallel to the surface has been carefully studied by Sanio in the normal cork formation in the cortex of ligneous plants, especially Dicotyledons, and will for these cases be more minutely described in Chap. XV[1]. In other cases there exist no detailed investigations of the succession of divisions. But one will hardly be wrong in assuming as the rule for the great majority of these cases the simplest of the types of succession distinguished by Sanio, that termed by him *centripetal*. In this the initial cell divides in the direction of the surface into two nearly equal daughter cells, of which the outer becomes directly a cork-cell, the inner a meristematic cell. In all the successive divisions which follow this, the same process is repeated, the outer cell always becomes directly a cork-cell, the inner remains meristematic. For the other types of succession also, which will be described in Chap. XV, the same general result holds, that at least to every mass of cork which grows to any considerable extent, new cork-cells are added from the meristem, which is to be found on its inner surface.

The average number of the strata of cells produced in one cork-layer is in the majority of cases small, the layer thus appears as a thin skin varying in thickness according to the special case from two to twenty cells. When this persists for a long time it retains nearly an equal thickness, since the outer layers die off and peel away. As this proceeds they are renewed from behind by the zone of meristem.

[1] Compare also there the figures relating to cork formation.

Thicker masses of cork, attaining a thickness of many centimetres, are formed on the cortex of Testudinaria elephantipes, and especially of the cork trees, which derive their names from it. These will be treated of in connection with the bark (Chap. XV).

The *cork-cells* remain uninterruptedly connected with one another. Only in the Melastomeae (Chap. XV), which form the first layer of cork on the margin of the bast, have intercellular spaces between the perpendicular edges of the cork-cells been observed. The form of the single cell is approximately that of a parallelopiped, usually with a five- to six-sided base, parallel to the surface covered by the layer. The height of the parallelopiped is usually smaller than the diameter of the bases, and the cells are thus more or less flattened, in extreme cases, to quite flat lamellae, as on the stem of Fagus, Betula, Tilia, species of Prunus, Boswellia papyrifera, &c. In other cases the radial and basal diameters are almost equal, or even the former larger than the latter, as especially in the soft cork of Quercus suber, Acer campestre, Ulmus, Aristolochia, &c., also in thin layers of cork, e. g. Philadelphus.

The basal diameters are in most cases about equal: in many forms, e. g. old stems of Betula, Prunus Cerasus, on the other hand, the cells are elongated considerably in a transverse direction.

The cork-cells of the above Melastomeæ form an exception to these rules, since they have the shape of elongated four-sided prisms, the sides of which are parallel to the longitudinal axis of the stem.

The single wall-surfaces remain flat and straight, or show archings and undulations. The latter holds especially for the lateral or radial faces of most of the less flattened cork-cells: indeed these are usually undulated in the radial plane: rarely (Pinus sylvestris, Larix [1]) in the tangential plane, so that the cell appears in surface view to have a star-like outline.

The structure and history of growth of the cork-cells are still but imperfectly known. The following facts, founded mainly on Sanio's investigations, may at present be stated on this point.

As regards the structure of the walls, one can distinguish firstly thin-walled cells with apparently almost homogeneous delicate walls, and others with thickened walls. Examples of the first are supplied especially by the iso-diametric or radially elongated cells of the soft masses of cork of the surface of the stem of Quercus suber, Acer campestre, Aristolochia, and the wide-celled layers of the bark of the Birch. The flat forms have usually, but not always (Nerium), thickened walls: and in that case the thickness of the walls is almost equal all round (e. g. Fagus, Boswellia papyrifera), or the outer (e. g. Salix, Zanthoxylon fraxineum) or the inner wall (e. g. Mespilus germanica, Viburnum opulus) is specially thickened: the thickening mass is either uniform or pitted. Fibrous thickenings are known in the uniseriate layers of thin-walled cells, which alternate with strongly thickened multiseriate layers, in the tough corky skin of Boswellia papyrifera [2]. The delicate membrane here shows narrow thickening bands, which protrude inwards, and branch here and there at an acute angle. Further, Sanio found in the cork-cells of the branches of Melaleuca

[1] Schacht, Lehrbuch, II. p. 572.

[2] Mohl, Botan. Zeitg. 1861, p. 229.

styphelioides a tangential annular thickening, which is uneven and wavy, and runs round the middle of the wall.

Corresponding to the usual conditions of structure of membranes, the thickening mass is in the cases of stronger thickening internally superposed upon a delicate homogeneous limiting layer ('primary membrane').

The membranes, which in the young meristematic stage are cellulose walls, appear in the mature cork-cell always *suberised* to a varying extent, i. e. composed of *cork substance*. Of the properties of this body we know that the suberised membrane shows, in its behaviour under reagents, and its coarser physical properties, specially its slight permeability for water, completely similar phenomena to the cuticle and the cuticularised membranes. Its chemical composition, and the statement that it contains nitrogen, which was found on the analysis of large masses of cork, are doubtful[1]. When examined microscopically the high refractive power of the suberised membrane is striking; its outlines appear dark and sharply marked in the illuminated field, from the time when the suberisation begins: thicker membranes (e.g. of the stems of the Birch or Beech) appear brightly luminous; in thinner ones one often observes as the microscope is focussed varying phenomena of colour[2].

According to the stage of the suberisation we may distinguish *totally* or *partially* suberised membranes, or layers of them. The former behave under reagents like cuticle (p. 74), cellulose cannot be proved present in them; the latter still contain cellulose even when old.

Often the wall is suberised all round and throughout its whole thickness: periderm of Fagus, Salix, and many thin-walled cork-cells on the surface of roots and tubers. On the other hand, the totally suberised mass often forms an outer lamella of the wall going all round, and it is lined internally by a layer of a different material, – partially or often perhaps not at all suberised,—which, after treatment with solution of potash, shows a clear cellulose coloration with iodine and sulphuric acid, or Schultze's solution. This lining is very slightly developed, only as an extremely delicate skin in the thin-walled cork-cells of Quercus suber and Betula. It is in this case only visible after not too strong warming with potash: continued boiling with this reagent destroys or alters it again: in Q. suber its destruction is accompanied by peculiar phenomena, which still remain to be carefully investigated. In many other cork-cells the cellulose-containing layer is to be seen, immediately within that which is totally suberised, as a less refractive mass applied to this internally, forming sometimes a thin layer equally thick all round, e.g. branches of Nerium, root of Rheum rhaponticum; sometimes a stronger thickening mass, equally thick all round (flat cork-cells of Boswellia papyrifera), or it is thicker on one side (Zanthoxylon fraxineum, Populus fastigiata, Platanus occidentalis). Without being acted upon by potash, it does not turn blue: in Platanus it turns blue after warming for a short time with this reagent; in the other cases named even after the reagent has acted for a few minutes without the temperature being raised. Most of the cork-cells

[1] On the chemical relations of cork, its products of decomposition, &c., compare the epitomes and citations of the literature in Hofmeister, Die Lehre von der Pflanzenzelle, p. 252; Wiesner, Rohstoffe, p. 479; Gmelin-Kraut, Handb. d. Chemie, VII. 1. p. 593; Husemann, Pflanzenstoffe, p. 1016.

[2] Compare Sanio, *l. c.* p. 57.

described by Sanio, which have an inner layer of the thickened wall of low refractive power, may be assigned to this category.

The presence within the totally suberised layer, which shows no cellulose reaction, of one showing cellulose-blue after treatment with potash, may explain Mohl's statement [1], according to which the cork-cells consist of cork substance and cellulose, and the presence of the latter may be proved by reagents after treatment with potash. The statement is correct for the cases just mentioned (I have not investigated all those enumerated by Mohl), but the blue coloration does not affect the whole suberised membrane, as Mohl asserts, but only the above described layer within that totally suberised. Also after treatment with Schultze's mixture no cellulose reaction appears in the latter. Moderate treatment with the mixture causes decolorisation and separation of the totally suberised membranes from one another. Stronger heating with it gradually changes the latter into a greasy disorganised mass [2]. Still stronger treatment with it dissolves it entirely.

Between the totally suberised outer layers of the wall of contiguous cork-cells there always lies a very thin limiting layer, the material of which differs in some way from them. Sanio describes this definitely for Ulmus effusa and Sorbus aucuparia, and figures the limiting lamella, from which in this case the totally suberised layers often separate in the section-cutting. It is distinguished from the latter by lower refractive index, but shows in other respects the same reactions. The fact that cork-membranes are separated from one another without injury when warmed with Schultze's mixture (Quercus suber), or even with potash (Boswellia papyrifera), is further evidence of the presence of such a delicate and distinct limiting lamella. On the question raised by Sanio of the possible growth of the membrane by apposition, these facts have at present no decisive bearing.

With the exception of a few points of difference, what has been above stated coincides with the facts recently discovered by Haberlandt [3]. He found in the cork of the cork oak, potato, elder, and maple a separation of the cells from one another after treatment with Schultze's mixture or chromic acid, and appearance of the cellulose reaction after treatment with solution of potash; the latter therefore, according to him, dissolves the cork substance combined with the cellulose, and the former reagents the 'Intercellular substance,' or limiting lamella, which he identifies with 'ligneous substance.' Whether the relations are so simple, needs further investigation, the more after what has been stated, since Haberlandt does not sharply distinguish the distinct cellulose-containing layer, which is present in the cell while still part of a continuous tissue.

As Mohl has shown, the fibrous thickened cells in Boswellia papyrifera are the only case as yet known of silicified cork membranes.

The *colour* of the cork membranes is independent of the stage and extent of the suberisation. The totally suberised membranes of old birch bark, of Salix viminalis, aurita, caprea, are colourless, those of Q. suber, &c. are bright brownish yellow, the internally thickened walls of Platanus greenish yellow: those of Salix alba, purpurea, and fragilis yellow; in general the colour of the membranes themselves is always very slight, and the bright brown colour of very many masses of cork is chiefly due to the cell-contents. The silicified walls of Boswellia, as far as it is possible to determine, are quite colourless.

[1] Botan. Zeitg. 1847, p. 503.

[2] Compare Schacht, Lehrb. I. p. 14.

[3] Ueber Nachweisung v. Cellulose im Korkgewebe. Oesterr. bot. Zeitschr. 1874, No. 8.

The suberisation of the walls begins, in the cases investigated, directly after the separation of the cork-cells by the divisions of the meristematic layer, and before the cork-cell has attained its definitive size and thickness of wall. In the above-mentioned Melastomaceæ, according to Vöchting, the wall even of meristematic cells still capable of division is suberised, provided the first divisions have once taken place. Where thickening masses slightly or not at all suberised appear within a totally suberised outer lamella, they appear, according to Sanio, later than the suberisation in the latter.

In accordance with its continued active growth, the young cork-cell is filled with protoplasm (nucleus) and cell-sap even after it has become differentiated by the occurrence of suberisation. Thus a young cork-layer, even when very completely developed, may remain transparent, and a branch covered by it (e. g. Tilia) may long appear green to the naked eye, by reason of the chlorophyll of the cortical parenchyma showing through it. Many cork-cells may remain for a long time in this condition of independent growth, e. g., those of Sambucus nigra, which last through the winter, and even form chlorophyll. Finally, and at most after a year, there appear important internal changes. In one case—especially in the thin-walled forms with large cavities—the contents dry up to insignificant residues, which often (Betula) attach themselves as granules to the wall: the space enclosed by the membranes is filled with air. In the other case the cavity is occupied by a dense, almost homogeneous, more or less darkly brown-coloured mass: I leave it as undecided whether this completely fills the space, as Sanio states, or whether air bubbles occur also. This is usually the case in flat, plate-like cork-cells, like those of the bark of Fagus, Castanea, Tilia, Pirus, &c.

When the air makes its appearance, the death of the cell has begun. The thin-walled cells and masses of cork, which are filled with air, are incapable of other than purely passive changes, and sink into gradual decay, e. g. Quercus suber, Ulmus, Betula, &c. Also in the case of the flat cells filled with brown contents it is probable that this mass consists of dead protoplasm and contents, and that the death of the cell is indicated by its appearance. It is at all events beyond doubt that in the stems, roots, &c. which grow in thickness, the cork-cells in question are finally torn and decay. On the other hand however these flat cork-cells, as in the above-cited trees, may be seen to increase for a long period in size in the direction of the periphery; there is a decrease it is true of the radial diameter, but not any great change of structure, or of the thickness of the walls. Destruction begins only at a later period, and with it the disappearance of the brown contents. Accordingly the question may be raised, and recommended for further investigation, whether the increase in size of these cells depends upon a purely passive extension, or is connected with a real growth, an increase in mass, at least of the walls.

In the larger masses of cork of many plants single cells, genetically equivalent to the cork-cells, assume the properties of short sclerenchymatous elements (compare Sect. 29), resembling in all important points the so-called stone-cells. The cork oak especially supplies examples of this, where such elements occur singly in all possible places, but especially near the lenticels (Chap. XV), and in the worse sorts of cork are known only too well by the dealers. Massive irregularly concentric zones of such stony, brown elements, alternating with numerous thin-

walled layers, characterise the corky masses of old tuberous stocks of Tamus elephantipes[1].

As has often been already indicated in what has been said above, the successive layers of one corky mass are either formed throughout of almost similar cells, or concentric zones of unlike properties alternate with one another.

The first case includes most cork-layers consisting as a rule of more or less flattened cells, which as thin skins cover wound-surfaces, roots, rhizomes, and the cortex of stems. The second case includes in part equally thin layers, e. g. those on the branches of Philadelphus, where one layer of cells greatly elongated radially always alternates with one to two layers of flat cells; on the other hand more especially thicker masses of cork, such as those of Tamus elephantipes, and the stems of dicotyledonous trees. The great flaps of cork on the cortex of Boswellia papyrifera consist, as already stated, of multiseriate layers of flat cells, which alternate with uniseriate thin-walled cells, with a fine fibrous thickening and silicified walls. A similar alternation of multiseriate layers of flat strongly-thickened cells and wide thin-walled ones occurs in the white corky covering of young birch stems, in the corky masses on the stems of Quercus Suber, Acer campestre, Liquidambar, &c. According to Hartig[2] and Sanio[3] each narrow-celled layer in the Birch corresponds to the inner limit of one annual increment of growth, as in the wood, only inverted (comp. Chap. XV)[4]. Also in Quercus Suber[5] the number of the concentric zones corresponds with the specified number of years through which the production of cork on the tree had lasted. Whether such relations between stratification and annual increment are more generally distributed remains still to be investigated.

It is manifest that the firmness or toughness of a layer of cork must vary according to the form and thickening of the walls of the cells, even if one assume that the physical properties of the corky substance are universally similar. As a fact, one finds the flat-celled, thick-walled layers firm and tough, resisting energetically both the increase of the enclosed parts and the causes of injury acting from without: the wide-celled thick-walled forms are soft, more easily burst by the increase of the enclosed parts, and more easily injured from without. Alternating wide- and flat-celled masses, as especially those of the Birch and of Boswellia papyrifera, peel off, when old, by splitting of the delicate wide-celled layers from one another.

According to Mohl's system[6], it is usual to distinguish the wide-celled softer form as *cork*, in the narrower sense, from the tough-walled masses of cork which are termed *Periderm*. Since this distinction can never be sharply drawn, it may here be entirely given up, and the above-described sort of tissue be termed *Cork* (Suber), while the term *Periderm* may be applied to all phellogenetic cortical products (to be more exactly treated in Chap. XV) of which the cork is a part.

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[1] Compare Mohl, Verm. Schr. p. 190. In the old specimens investigated the hard layers are much stronger according to Mohl's statements than in the younger ones.

[2] Forstl. Culturpfl. p. 306. [3] *l. c.* p. 83.

[4] Von Merklin, Mél. Biolog. de l'Acad. S. Pétersburg, opposes Hartig's statements.

[5] C. de Candolle, in Mémoires de la Soc. de Physique de Génève, XVI. p. 1 (1861).

[6] Verm. Schr. p. 212.

SECTION III.

PARENCHYMA.

Sect. 25. The term *Parenchyma* is here applied to all internal *cellular* tissue, *i. e.* that which is found within the epidermis or cork-layer. Though as a fact it is in the main identical with Sachs' *ground-tissue* (p. 6), in conception it is not so.

It has already been stated (p. 5) that in this limitation and classification of tissues the distinction is drawn between those elements which *retain their cell-nature*, and such as have lost that character. Attention was also drawn to the difficulty in the way of a generally uniform distinction, partly from the incompleteness of our present knowledge, partly from the undoubted occurrence of real intermediate forms between cellular tissue and many distinct tissues, especially Sclerenchyma. These difficulties did not come prominently forward in Sections 1 and 2. Here, in the internal tissues, they appear frequently, and it is everywhere to be repeatedly pointed out that in the distinctions about to be drawn, definite types must be indicated, which recur universally, but are never sharply distinguished from one another. As regards the distinction of *cells* from other tissue-elements resulting from the metamorphosis of cells, it may here be again called to mind that the former are distinguished from the latter by the permanent protoplasmic body, in which the nucleus also (always?) remains, or appears temporarily. With these parts, which are directly observable anatomically, the cells retain the faculty of active growth and of division: it is true that this faculty is often enough not manifested, but, in the processes of secondary thickening (comp. Chap. XV), and especially in the phenomena of formation of cork (Sect. 24) brought about by wounding, it may be so generally observed, that it may serve as a very useful character. The chlorophyll-containing parenchyma of a foliage-leaf, for instance, after complete unfolding shows as a rule no further division: the smallest wound immediately induces it. In very thick-walled, sclerotic cells, the direct anatomical determination of protoplasm and a nucleus is difficult, and as a fact is often impossible. Nor is that of the power of division more practicable. In its stead another phenomenon is to be taken into account, namely the periodic appearance and disappearance of starch-grains in many elements, which judging from the nature of their walls may be doubtful. Putting out of account the sieve-tubes (Chap. V), and certain laticiferous tubes (Chap. VI), in which, at all events, peculiar conditions, which need not here be touched upon, are the rule, the formation of starch in all well-known cases is directly connected with an active protoplasmic body. In doubtful cases therefore it is to be regarded as a character which indicates the presence of such a body, so long as it is not proved that it can also occur in spaces without protoplasm, and surrounded by cell-membranes. Abundant starchy contents, and especially periodical changes in their amount, must therefore for the present be regarded as a criterion of the cell-quality. In Chap. XIV we shall again return to this subject.

Respecting the *structure* of the cells of the parenchyma, nothing *general* need be brought forward at present, which would not be included in the doctrine of the structure of the mature vegetable cell, and this we assume to be already known.

As was stated in Sect. 1, their *form* is extremely various, and we may here distinguish as the chief types the iso-diametric, or *short* forms, and the elongated—*fibrous cells, fibrous-parenchyma* ('Prosenchyma'). The further distinction of forms, to which during a certain period much energy was devoted[1], has at the present day hardly even an historical interest. However certain definite forms, which are characteristic for definite single cases, must be mentioned.

As is the case in cellular tissue generally, the special structure may be taken into consideration, and the distinction may be drawn between *thin-walled* and *thick-walled parenchyma*, according to the relative development of the membrane on the one hand, and of the protoplasm and cell-contents on the other; but this holds only in extreme cases. In the distinction of subdivisions, the manner of connection of the cells one with another is taken into consideration as one of the characteristic special relations of structure.

Thin-walled parenchymatous cells are in most plants the organs of the process of assimilation, and the storehouses of its first products; besides having a relatively thin membrane they are therefore usually distinguished by their contents; *viz.* assimilating chlorophyll, and the most widely-spread direct product of assimilation, starch. According to the preponderance of one or the other of these parts, we may speak shortly of *chlorophyll parenchyma*, *starch parenchyma*, in many other cases of *oil-containing parenchyma*, &c. The parts of plants which contain chlorophyll, and in which reserve products are laid up, e. g. especially the leaf, cortex of stems, and Rhizomes, are the places where these cells occur in large masses.

In contrast to those characterised by the parts of the protoplasm and contents appearing as above described, there are other thin-walled parenchymatous cells, in which, within a protoplasmic sac, which is usually very delicate and slightly developed, all the solid constituents of definite form diminish till they disappear entirely before the cell sap; this sap fills almost the whole of the cell, and is watery, or contains very thin mucilage. This may accordingly be termed *sap-parenchyma*. This is wide spread, and as 'aqueous tissue' has recently been thoroughly described by Pfitzer[2] in many thick long-lived foliage-leaves, in which it is situated beneath the epidermis (hypoderma), forming as it were layers strengthening the latter, as in the Pleurothallideæ, Bromeliaceæ, Ilex, Nerium, &c.; or it appears as a middle layer of the leaf, and is surrounded by chlorophyll-parenchyma, as in many succulent plants, e. g. species of Aloe and Mesembryanthemum, and in the leathery leaves of species of Callistemon, Hakea, &c., which will be more fully described in Chap. IX. It occurs in specially large masses in parts without chlorophyll which are rich in inulin or sugar, such as tubers and roots of Compositæ, Campanulaceæ, Beta, &c. The cells in question are characterised by their contents, which are almost perfectly transparent and fluid, being sometimes watery, sometimes (species of Aloe) mucilaginous. Their chemical constituents are exactly known only in single cases, as in the above Compositæ and Beta, they cannot therefore at present be used in distinguishing them generally.

[1] Hayne, in Flora, 1827, II. p. 601.—Meyen, Phytotomie, p. 63.—C. Morren, Bull. Acad. Bruxelles, tom. V. No. 3.—Compare Mohl, Veget. Zelle, p. 15.

[2] Pringsheim's Jahrb. VIII. p. 16.

The forms of thin-walled parenchymatous cells are in the main nearly iso-diametric; but there often occur also elongated-prismatic, spindle-shaped cells, and the like, examples of which, e. g. in the case of the vascular bundles, will be described later; to this category belong also those chlorophyll-containing cells arranged in many leaves perpendicular to the surface, forming the *palisade parenchyma*, to be described in Chapter IX.

As above intimated, very great variety of shape is found among the iso-diametric forms. It is only in definite single cases, e. g. in hypodermal sap-parenchyma, that the cells are of such form that all of them are bounded by flat surfaces and sharp edges, and therefore are in uninterrupted connection with one another. As a rule the surface of the parenchymatous cells is more or less rounded, or bears irregular protuberances, or the protuberances themselves are drawn out into long arms: in this case they are mutually connected only by definite parts of their surface, which vary in size according to the special form. Between them intercellular spaces are left free. Masses of parenchyma in which the latter (which are then usually filled with air) are developed to a great extent are distinguished as *lacunar parenchyma*, or, comparing it with a bath-sponge, *spongy-parenchyma*. Compare Chapters VII and IX.

The walls of the cells of this category are as a rule cellulose membranes, with ordinary simple pitting. The latter, following the general rule, usually occurs only on the parts of the surface in contact with that of other cells: in cases then where the cells show a decided partial rounding off, and only touch one another with narrowly limited parts of their surface, or only with the ends of protuberances, the pits lie on these spots, and not on the rest of the wall. As regards the surfaces of contact, the same may also occur with dissimilar tissue-elements. When similar cells touch one another by the ends of narrow protuberances, there is often only a single pit on each protuberance; larger circumscribed surfaces of contact appear as pitted fields on the otherwise smooth wall (Fig. 46). This phenomenon, which was known long ago[1], and which occurs especially often in round-celled chlorophyll-parenchyma of succulent plants, resembles that of the sieve-plates of the sieve-tubes (Chap. V); but it is incorrect to place it side by side with this[2], since the characteristic structure of sieve-plates is wanting in the parenchymatous cells, though the pitted fields also in the parenchyma of the leaf of Cycads, specially of Encephalartos, are distinguished from the rest of the wall by brown coloration in Schultze's solution, and deep red coloration in solution of Anilin[3].

FIG. 46. A parenchymatous cell from the cotyledon of Phaseolus multiflorus, isolated by maceration; *ii* the parts of the wall where it borders on intercellular spaces, *tt* the pitted parts of the surface which border on neighbouring cells, the thinnest points of the pits are shaded dark (550). From Sachs' Textbook.

Fibrous partial thickenings of the walls are known here and there, e. g. in the form of reticulate or spiral fibres, in the watery hypodermal parenchyma of the leaves of the Pleurothallideæ, and in many roots of orchids; as reticulate fibres in the

[1] See *e. g.* Schleiden, Grundz. 3 Aufl. I. p. 245.

[2] Areschoug, Botan. Zeitg. 1870, p. 305; and Acta Univ. Lund. tom. IV.—Bořčzow, in Pringsheim's Jahrb. tom. VII.

[3] Kraus, Cycadeenfiedern, *l. c.*

middle layer of the leaf of Sanseviera guineensis; as longitudinal fibres in the chlorophyll-parenchyma of the leaf of Cycas[1]. They appear in an exquisite form in the parenchyma of the primary transient cortex of the root of most Coniferæ (with the exception of all the Abietineæ); this tissue may be best placed in this category[2]. The cells of the concentric layers of parenchyma, which lie outside the endodermal sheath (§ 27), are in many forms all finely reticulated (Phyllocladus, Podocarpus sp.), or thickened with coarse nets and longitudinal fibres (Cupressus spec., Sequoja sempervirens); in Torreya nucifera this thickening is limited to the 2–3 outermost layers, and the innermost layer bordering on the endodermis. In most of the investigated forms, as Taxus, Biota, Thuja, only the latter layer has a fibrous thickening, and, as also in Torreya and Cupressus, each of its radial walls has in its middle one straight, thick, stratified, half-cylindrical, longitudinal fibre, which is continuous over the transverse walls into that of the opposite radial wall, and in all cases fits exactly on to a similar thickening of the neighbouring cell. In Thuja occidentalis this fibre contains resin according to Reinke. The layer of cells thickened in this manner appears as a closed sheath, with the exception of Frenela rhomboidea, where, according to Strasburger, it shows a break opposite both ends of the row of vessels (Chapter VIII).

As a special case, to a certain extent worthy of mention, the tabular-polyhedral chlorophyll-cells peculiar to the leaves of species of Cedrus and Pinus[3] and many Gramina[4] may be further cited: these have narrowly infolded bands of wall, and from them broad ridge-like thickenings of the wall protrude inwards. Compare above, pp. 35, 78; figs. 11, 27.

Luerssen[5] has recently proved that partial thickenings of the walls *protruding on the outer surface* are a characteristic phenomenon for the parenchyma of many ferns. They occur in the chlorophyll-parenchyma of the leaf of the investigated Marattiaceæ, and in the parenchyma of the petiole of the same plants, as well as of numerous investigated Cyatheaceæ, Polypodiaceæ, and of Todea barbara. They also occur in the stems which have been investigated with reference to this point, e. g. in Ophioglossum vulgatum, species of Polypodium, and Pteris (Luerssen), Aspid. filix mas, Onoclea struthiopteris, Cyathea arborea, Imrayana, Alsophylla microphylla; in Marattiaceæ, e. g. M. Kaulfussii, also in the cortex of the root. In most ferns they appear to be wanting in the chlorophyll-parenchyma of the leaf. The protrusions of the outer surface occur obviously only on those parts of the wall which border on intercellular spaces, and, as a matter of fact, only on air-containing intercellular spaces. In comparison with the thickness of the rest of the cell-wall they are always thin, and when slightly developed they appear in the form of small knots, when better perfected as fine filiform rods, rarely thickened like clubs at their ends; the longer ones are not uncommonly branched. In relatively few cases they occur

[1] Compare Hofmeister, Pflanzenzelle, p. 168.

[2] Van Tieghem, Ann. Sci. Nat 5 sér. XIII. p. 187.—Strasburger, Coniferen, p. 346.—Reinke, Morpholog. Abhandl. p. 35.

[3] Meyen, Physiologie, I. Taf. VI. 17.—Hartig, Forstl. Culturpfl. Taf. 18.—Thomas, in Pringsheim's Jahrb. IV. p. 40.—Compare also Hofmeister, Pflanzenzelle, p. 169.

[4] Karelstschikoff, Bullet. Soc. Imp. de Moscou, 1868, No. 1.

[5] Botan. Zeitg. 1873, p. 641, Taf. VI.—Sitzungsbr. d. naturf. Ges. zu Leipzig, 1875, No. 7.

singly, e. g. rhizome of Ophioglossum, petiole of Dicksonia antarctica. Usually they are numerous and closely aggregated. The elongated rods springing from the different sides of the intercellular space in all directions are irregularly intertwined between one another, so as to form a delicate framework with air in its inter-spaces. The single rods sometimes end free, sometimes they are connected by their branches, or go from one side of the intercellular space to the opposite, and also adhere to the latter. As regards their material, the above outgrowths of the wall are equivalent or similar to 'slightly cuticularised membranes.' Cellulose colourings cannot be observed in them, but rather they and the outermost layer of membrane which connects them both behave under reagents like the limiting lamellæ on the surfaces of contact of the contiguous cells; they turn yellow or brown with Schultze's solution, or with iodine and sulphuric acid, and are destroyed by boiling with solution of potash. It remains for further investigation to determine how far they may accordingly be styled parts of an inner cuticle lining the air-passages.

Sect. 26. A definite special form of *thick walled parenchyma* is distinguished by the name *Collenchyma*[1]. It forms thick bands beneath or near to the epidermis, especially in stems, petioles, and nerves of the leaf of herbaceous Dicotyledons (e. g. species of Rheum, Rumex, Beta, and Chenopodium, Aegopodium, herbaceous shoots of Sambucus, Labiatæ, Solanaceæ, Begonias, petioles of Nymphæa, etc.[2]), and in the petioles of the Marattias[3]. In their typical development it is distinguished by the form and structure of the walls of its cells, which are capable of division and contain chlorophyll. The cells are in unbroken connection with one another; only in exceptional cases (stem of Silphium conjunctum and its allies) are the layers traversed longitudinally by intercellular canals. In form the cells are elongated many-sided prisms, with horizontal or obliquely pointed ends: when they are isolated it is usually plain that they are derived from elongated mother-cells, with sharply pointed ends, which are divided by permanently thin transverse walls, or, as the case may be plainly stated, they are chambered[4]. The walls are thin at the ends, and along the whole of the middle of the lateral surfaces of cells, which face similar cells; but along the angles they are provided with a stronger thickening, which protrudes into the cavity of the cell so as to round it off, or it may even project further, while towards the thin middle band of the wall it is sloped off, or sharply truncated (Fig. 47). In the stem of the above-named species of Silphium the thickening extends also over the faces opposite the intercellular spaces. The

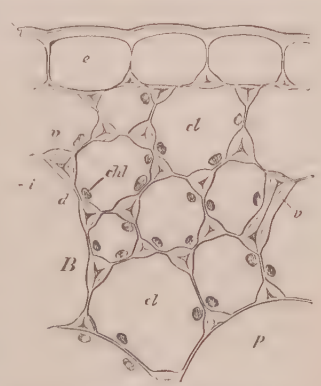

Fig. 47. Epidermis, *e*, and collenchyma, *cl*, of the petiole of a Begonia. The epidermal cells are evenly thickened on the outer wall, where they abut on the collenchyma; they are thickened like it at the longitudinal angles where never three cells meet, *cll*. Chlorophyll grains, *p* thin-walled parenchymatous cells (550). From Sachs' Textbook.

[1] [Cf. Giltay, Botan. Zeitg. 1881, p. 153; also 'Het Collenchym,' Utrecht.—Ambronn, Pringsheim's Jahrb. XII p. 473.—Van Wisselingh, à la conaissance d. Collenchyme, *Ref* Bot. Centralblatt, 1882, Bd. XII. p. 120.]

[2] Compare Mohl, Vegetab. Zelle, p. 20; Botan. Zeitg. 1844, p. 308.—Unger, Anat. und Physiol. p. 148.—Sachs, Lehrb. p. 24.

[3] Russow, Vergl. Unters. p. 106.

[4] Compare Kraus, Cycadeenfiedern, *l. c.* p. 310 (6).

thickened parts of the walls have no pits, and are delicately stratified with very fine limiting layers ('Intercellular-substance'): they swell largely with water, but without becoming gelatinous; when water is removed they contract greatly in all directions (measurements are wanting). In the soaked condition they show, in transmitted light, a characteristic bluish white lustre. With Schultze's solution they turn light blue[1]; after slight warming with potash they immediately turn deep blue with solution of iodine in potassium iodide (this is the case in Sambucus, Rumex, Lamium album, Cactaceæ, Nymphæa).

In the same places which are occupied in many plants by cells thus remarkably characterised by the above described properties, there are found in many others layers of cells which differ more or less from these in their form and in the structure of their elements. For instance, the cells of the Collenchyma of the stems of Cacti already mentioned[2] differ from those described as typical, in their slight elongation, and in the fact that the walls are thickened strongly and uniformly all round, and coarsely pitted. Other single forms approach nearer to the thin-walled or sclerotic forms of parenchyma, without its being possible to carry through any sharp distinction. It is then to a great extent a matter of taste how far one will extend the term Collenchyma. It is now used generally for the form of tissue here described as typical, though it was originally proposed by Link[3] for the pollen mother-cells with their gelatinous membranes, and was then transferred by Schleiden, at first half in joke, to the above-mentioned collenchymatous cells of the Cactaceæ.

From the collenchyma must be distinguished the thick-walled forms of parenchyma, the membranes of which are more or less lignified, and have thus become hard and *sclerotic*. As the most typical representatives of tissue of this sort may be brought forward the thick-walled cells of the secondary wood of Dicotyledonous trees, which lay up starch periodically, and often prove themselves capable of division in the case of wounds, or rather healing scars. This will be entered into in more detail in Chapter XIV. In other places than that just mentioned sclerotic cells are to be found widely spread: together with collenchyma and sclerenchyma they form the strengthening apparatus of those parts, and they are connected with both of these tissues by the most various transitional forms. No general specific peculiarities of this tissue can be mentioned in addition to what has been already said; remarkable examples will therefore for the most part be mentioned in the chapters which deal with the distribution of tissues. Here we may briefly notice only one series as being specially instructive, and as presenting difficulties in a sharp classification of the tissues, viz., that of the sclerotic cells in the Ferns. In the large majority of these plants there occur in stem, roots, and leaves thick-walled elements, sometimes isolated, but usually in close and often in uninterrupted connection with one another, and combined to form uniseriate or multiseriate layers or bundles; these either lie near the epidermis, or accompany or ensheath the vascular bundles. In the petiole of the Marattiaceæ they have the properties of collenchyma, as was above stated; also many bundle-sheaths, to be cited later, are directly connected with this tissue as regards their structure. But in the large majority of cases (compare Fig. 48) the walls, which

[1] Schacht, Lehrb. p. 195.

[2] Compare Unger, Grundzüge, p. 25; Schleiden, Anatomie d. Cacteen, p. 14.

[3] Grundlehren d. Kräuterkunde, II. p. 199.

are equally thickened all round, or less thickened on one side, are highly 'lignified': in some few cases they are quite or almost colourless (e. g. stem of Lycopodium), usually they are coloured a dark brown. On the chemical property of the characteristic brown substance nothing certain is known. The sclerotic-tissue elements are generally of elongated prismatic form, either with slightly inclined or sharp-pointed ends, in the latter case they are fibrous cells or fibres. According to the character of their contents, they must, in compliance with the fundamental ideas above laid down, be for the most part assigned to the category of cellular tissue, since most of the elements, even those with very thick walls belonging to the dark brown layers and strands in the ferns, are densely filled with starch grains, which (as was observed in rhizomes of Osmunda regalis) gradually disappear as their age increases. It was not possible by any means to prove that these cells are capable of division. On the other hand, there occur side by side with these sclerotic cells, and often connected with them by quite gradual transitions, elements thickened till the cell cavity almost disappears, and showing only the last traces of cell-contents. These, regarded independently, should be accounted as specific sclerenchymatous fibres; thus, e. g. in the brown sclerenchymatous sheath of the stem of Marsilia salvatrix.

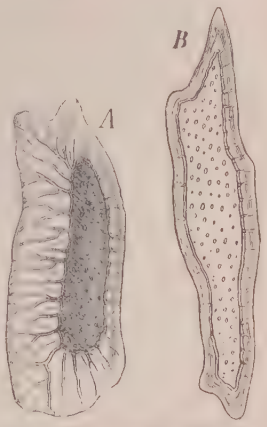

Fig. 48. Two sclerotic brown cells from the hypodermal layer of the rhizome of Pteris aquilina, isolated by chlorate of potash and nitric acid. *A* more strongly thickened on one side and with branched pits (350). *B* less thickened, the optical section of the wall and the pitted wall at the back are drawn in. From Sachs' Text-book.

Sect. 27. The name *Endodermis*, proposed by Oudemans[1] for a special case, here denotes generally those peculiar limiting layers to which Caspary[2] has given the name *protective-sheath* (Schutzscheide)[3]. They belong to the category of cellular tissue by reason of the nature of their contents, and their power of independent growth and division, which is so often to be observed, e. g. in roots of Dicotyledons.

The endodermis is a sheath consisting in all cases of one single layer of cells. It should also be observed here, that it lies as a rule at the limit between masses of parenchyma and other systems of tissue, especially vascular bundles; and is then to be recognised both by its development and its mature properties, as the layer of the parenchymatous mass bordering on the unlike part. In roots with an axile vascular cylinder the latter is always enclosed by it. The same is the case in stems with an axile vascular cylinder, as Hippuris, Callitriche, Ceratophyllum, Utricularia, Elodea, species of Potamogeton, Corallorrhiza, &c. (compare Chapter VIII), or with a closely compressed axile system of bundles (species of Potamogeton, Hydrocotyle vulgaris, &c.): also in stems of Phanerogams with a strongly developed cylinder containing the vascular bundles, this is marked off from the surrounding mass of parenchyma by a layer of endodermis, e. g. Tagetes patula, and other Compositæ[4], Cobæa scandens,

[1] Ueber den Sitz der Epidermis bei den Luftwurzeln der Orchideen. Abhandl. d. Acad. Amsterdam. Math. phys. Klasse IX (1861).

[2] Pringsheim's Jahrb. I. p. 441; ibid. IV. p. 101.

[3] [Cf. also Schwendener, Die Schutzscheide u. ihre Verstärkungen, Abhandl. d. Königl. Akad. d. Wiss. zu Berlin, 1882.]

[4] Van Tieghem, Ann. Sci. Nat. tom. XVI. p. 113.

Primulaceæ, as Primula sinensis[1], Lobelia syphilitica, Rhizomes of Scitamineæ, Cyperaceæ (e. g. Carex hirta), Acorus gramineus.

The same occurs in certain Equiseta. But on the other hand not the whole body of vascular bundles, but each single vascular bundle is in many cases sheathed round by an endodermis. This is the case both in the stem and leaf of almost all ferns and many species of Equisetum, and also in the petioles and leaves (Adoxa moschatellina, Menyanthes trifoliata, species of Primula), and in many stems of Phanerogamic plants, as Nuphar, Brasenia peltata, Hydrocleis Humboldtii, Primula auricula, Menyanthes. Rarely an endodermis occurs in other places than those named: thus in the parenchyma of the stem of many Equiseta, and in many aerial roots, especially of epiphytic orchids, the parenchymatous cortex is marked off both from the vascular bundle and from the tracheal sheath by an endodermis.

The relations in the species of Equisetum may here be described according to Pfitzer[2], as being specially instructive for the arrangement of the endodermis, which is variable even in closely allied plants. In the parenchymatous ground-mass of the internode there is a ring of vascular bundles equal in number to the angles of the stem (comp. Chap. VIII). In the foliage-stems of E. limosum and E. littorale an endodermal layer surrounds each single bundle. In E. arvense, Telmateja, silvaticum, pratense, palustre (comp. below, Chap. VIII), and scirpoides, this sheath is wanting round the single bundle, but surrounds the whole ring externally, curving inwards between two bundles. Besides this outer general sheath, there occurs in E. hiemale, trachyodon, ramosissimum, and variegatum a similar inner one, i.e. one bordering the whole inner side of the ring of bundles. In the rhizomes the same phenomena occur on the whole as in the foliage-stem; but in the same species, as more minutely described by Pfitzer, the rhizome and foliage-stem may be similar or dissimilar. Finally, at the points of transition between rhizome and foliage-stems, Pfitzer often found in E. hiemale small strings of parenchyma 1–3 cells thick, as seen in transverse section, which lay between two vascular bundles, and were surrounded by an endodermal layer, the latter either arising as a protrusion from the general sheath, or having no connection with it.

The cells of the endodermis (see Figs. 49 and 50) are nearly of the four-sided prismatic form, very often flattened in the direction of the tangent of the part enclosed by them, more or less elongated, with horizontal or oblique ends, and connected uninterruptedly with one another along their radial lateral faces. Their membrane is always delicate when differentiation of tissues begins, and often throughout life it is smooth externally and internally, rarely it is delicately pitted; but the radial walls are characterised by a fine and usually irregular wavy transverse folding, which is continued over the ends from one radial wall to the other. Further, the undulation extends, according to the special case, either over the whole surface, or only over a band-like longitudinal strip of it.

The wall of the cells is further characterised by suberisation, which appears early, i. e. with the first differentiation of tissue: this always affects the undulated part of the wall, and may also extend, according to the special case, in varying degree over some or all of the other walls. This is the case in the majority of Ferns: a good example of the localisation of the suberisation on the undulated bands in the middle of the radial (cellulose) walls is supplied by the root

[1] Von Kamienski, Vergleichende Anatomie der Primeln, *l. c.*

[2] Ueber d. Schutzscheide der deutschen Equiseten, Pringsheim's Jahrb. VI.

of Botrychium Lunaria. In the root of Ranunculus Ficaria Caspary found most of the cells suberised, more particularly at least on the undulated walls; and, on the other hand, single cells, with no exactly definable arrangement, equally suberised all round. The walls in question may be termed suberised on this ground, viz. that they behave before reagents like the totally suberised membranes of the cork-cells, or like cuticle. (Comp. pp. 75 and 111.) They alone remain behind after the action of concentrated sulphuric acid, even if the acid has destroyed the surrounding cellulose walls. More exact investigations of its chemical relations are entirely wanting. Further, the peculiar refractive properties of corky walls, the dark black contours when seen by transmitted light, belong to the walls in question. Partly in

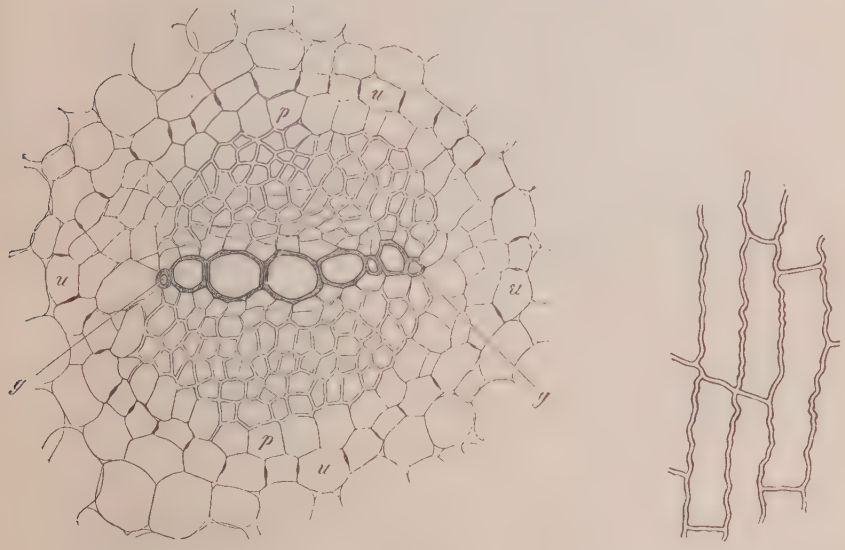

FIG. 49.—Ranunculus fluitans; transverse section through the vascular bundle of a strong old adventitious root (225). *u* endodermis, *p* pericambium, *g* outer primordial vessels of the diarch uniseriate xylem *g*—*g*; between *g*—*g* and *p* the phloem.

FIG. 50.—(375) A piece of the endodermis in tangential longitudinal section.

this circumstance, partly in the wavy folds superposed one on another, in not very thin preparations, lies the cause of the often-described phenomenon, that the undulated strips of the radial walls appear in transverse sections as dark points or lines. Another peculiarity, which again recalls the cuticle, is this, that the suberised parts of the walls swell in sulphuric acid and in potash in the direction of their surface. The undulations appear after the action of those reagents to become higher; but whether this is really the case, or whether they only become plainer for observation, remains to be investigated.

Like many cork-cells, those of the endodermis often remain thin-walled throughout life, e. g. in almost all Ferns, the walls being either totally suberised, or (a point which requires more extended investigation) having a delicate internal cellulose layer. But on the other hand, there appears not infrequently here also a strong thickening superposed internally on the original membrane: this occurs especially in roots of Monocotyledons, the stems of Potamogeton (in many species, as

P. crispus, densus, gramineus, no strong thickening occurs), rhizomes of Cyperaceæ, e. g. Carex hirta, exceptionally also in roots of Dicotyledons (Primula Auricula). Comp. Fig. 51. In many rhizomes of Monocotyledons, e. g. Carices, several thick-walled sclerotic layers occur in the region occupied in allied plants by the endodermis, when fully developed: it remains to be investigated how far these are endodermis.

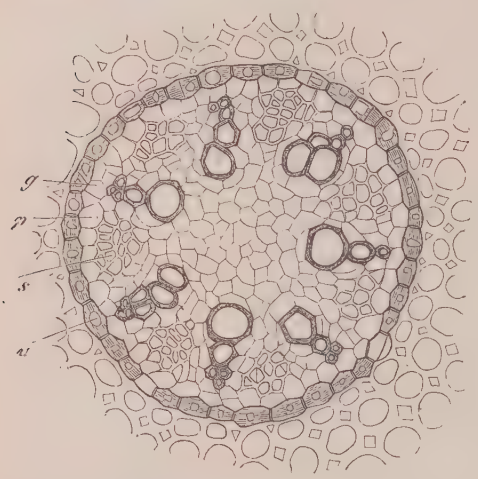

FIG. 51.—Primula auricula (225); transverse section through the heptarch vascular bundle of an adventitious root and its surroundings. *p* pericambium; *g* the outer primordial vessels of the vascular rays, which alternate with the seven phloem-groups, and are separated from these by thin-walled parenchyma; *u* endodermis; outside this is rather thick-walled cortical parenchyma, with intercellular spaces tetrangular in transverse section.

The thickening masses are as a rule more or less sclerotic—lignified, or suberised—only in Pr. Auricula do they consist of cartilaginous, gelatinous cellulose. In relatively few cases they extend in equal thickness round the whole cell (root of Pr. Auricula, of many epiphytic Orchids, stem of Potamogeton pusillus); usually they are more strongly developed on the inner side, than on the outer; roots of species of Carex, Cyperus, Scirpus, Phragmites communis, Triticum repens, Asparagus, species of Smilax (the so-called core-sheath (Kernscheide) of Sarsaparilla roots), Dracænas, Palms[1], and in the above-named rhizomes of Cyperaceæ, the stems of Potamogeton pectinatus, lucens, natans, prælongus[2]: comp. below, Chap. VIII. The thickening masses are stratified and pitted; only in the investigated Dracæneæ they are not pitted (Caspary). The undulation is not present on the thickened walls, but it again appears on the original radial walls, if they can be isolated by destruction of the superposed thickening masses, e. g. by sulphuric acid. Usually the thickening and sclerosis extend to all the cells almost equally, but thin-walled cells often occur between the others. They are found quite solitary, e. g. often in the root of Auricula (Fig. 51); or numerous, but alternating not very regularly with the thick-walled cells, in the root of Strelitzia ovata. But in the vascular-bundle-sheath of the aerial roots of epiphytic Orchids 1–2 longitudinal series of cells remain before each vascular group with an unthickened membrane, which turns blue with iodine and sulphuric acid: in their longitudinal course they are here and there interrupted by thickened cells[3].

The elements of the endodermis are, in all exactly investigated cases, cells in the fullest sense of the word, with a protoplasmic body; in Equisetum, according to

[1] Caspary, *l. c.* p. 108.—Schleiden, Archiv d. Pharmac 1847.—Berg, Atlas d. Pharm. Waarenkunde, Taf. III, IV.—Mohl, Palm. structura.—Karsten, Vegetationsorgane der Palmen, Taf. III. fig. 2.

[2] Caspary, Pringsheim's Jahrb. I. p. 443.

[3] Leitgeb, Wiener Acad. Denkschr. Bd. 24, p. 207.

Pfitzer, they even contain chlorophyll; further, as in all parenchymatous cells, the nature of their contents is very various; many are poor in contents of definite form, or almost empty; very many have abundant starch grains, and even to a remarkable degree in comparison with the surrounding parenchyma. Also in strongly thickened and sclerotic cells there are often abundant starchy contents, as in the roots of Cladium Mariscus, and Carex arenaria according to Caspary, in the stem of Potamogeton natans, &c. In single cases, namely, in roots of Ficaria and Victoria regia, and in stems of Equisetum, Caspary and Pfitzer found the protoplasmic body of the cells brown, and contracted to a band stretched between the undulated walls.

As was already indicated at the outset, the layer of cells limiting the parenchymatous cortex from the air-containing sheath, which surrounds it in the aerial roots of the epiphytic orchids and Aroideæ, of Chlorophytum and Hoya carnosa, is a special case of endodermis. It corresponds in all important points with the 'protective sheaths,' and is generally distinguished by one peculiarity only, that in each of the longitudinal series, which its cells form, elongated prismatic elements alternate regularly with short roundish or oval cells. Usually all the cells have thin walls, and in that case (according to Leitgeb always) they are undulated on their radial faces; they have, as far as my investigations extend, a complete suberised outer layer, and a delicate cellulose inner layer. But in many species the long cells are strongly thickened and sclerotic, most strongly, and without pits in Oberonia myriantha (Leitgeb, *l. c.*). The short cells are always thin-walled. The long cells contain chiefly watery cell sap. The short ones are characterised by relatively abundant, granular protoplasm, and a large nucleus. On the structure of the roots in question, comp. Sect. 56.

CHAPTER II.

SCLERENCHYMA.

Sect. 28. The name **Sclerenchyma**, introduced by Mettenius[1], here indicates those tissue-elements which have not only thickened their walls at the expense of the cell-cavity, but have also lost the cell quality besides. Together with the sclerotic cells of the foregoing paragraphs they form the strengthening apparatus. But while the former, by reason of the nature of their contents, still take an active part in the processes of assimilation and nutrition, the properties which point to this are wanting in the tissues in question; they appear (besides some connection with the transfer of water) to be in the main only strengthening apparatus, or specific mechanical elements, to use the terms of Schwendener.

We will not here again return to the practical difficulties in distinguishing this tissue from the sclerotic cells. Comp. p. 115, and Chap. X.

The general properties of the sclerenchymatous elements consist in this, that as the thickening and lignification proceed, the protoplasmic body and nucleus disappear, and of these and of the products resulting from their activity only remnants together with watery fluid remain behind, partly as not clearly defined granular contents; often however they take the form of rather abundant fine-grained starch, which apparently has no further use, as e. g. in the fibrous ring of the outer walls of Aristolochia Sipho, or of crystals of Calcium oxalate, as in many covering tablets of fibrous bands, to be described below, and in the raphide-containing fibres of the cortex of the root of Chamœdorea elegans. According to Schwendener[2] a part of the fluid contents is replaced in the typical sclerenchymatous fibres by air; they always contain some air in the normal condition. The structure of the walls is in general that of strongly thickened cell-membranes, with their numerous modifications: these will be more readily described in connection with the single forms.

According to the form, and the definite relations of structure which vary for the most part with it, we may distinguish two main forms of sclerenchymatous elements, which, however, are not in all cases sharply defined from one another, viz. (1) short sclerenchymatous elements, and (2) elongated elements, or sclerenchymatous fibres.

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[1] Abhandl. d. K. Sächs. Ges. d. Wissensch. IX. p. 432.

[2] Das Mechanische Princip, &c., p. 110.

Sect. 29. The term **Short sclerenchymatous elements** may be applied to all forms which have not pointed tapering ends; these are sometimes iso-diametric, sometimes moderately elongated. To this group belong—

(*a*) The *stone-elements* ('stone-cells' of the Pharmacologists), so called after the stony bodies in the flesh and stalk of many pears, which are composed of them, are almost iso-diametric, rarely rod-like elongated derivatives of cells ('rod-cells'), with stratified, very strongly thickened membrane, lignified to a stony hardness: this wall is perforated frequently by numerous, usually branched pit-canals, of circular appearance in transverse section (Fig. 52). The narrow internal cavity, which usually disappears, is occupied by a watery fluid with a few granules, or often by a reddish brown, apparently formless mass. Stone-elements of this sort are widely spread among the Dicotyledons, especially in sappy, fleshy parts; in the succulent parenchyma they are sometimes isolated, but usually in uninterrupted connection with one another, forming circumscribed groups, or masses, of which the elements bordering on the thin-walled tissue may graduate into the latter by the thickening of their walls at this limit being one-sided and weaker. In the so-called stout succulent plants, however, such as the Crassulaceæ, Cactaceæ, &c., stony formations are generally wanting. Exquisite examples are supplied by the fleshy body of Helosideæ, Lophophytum, Langsdorffia[1], fleshy tuberous roots, e.g. Pæonia, Dahlia (Sachs); Rhizomes, e. g. Dentaria pinnata, the pith of Hoya carnosa[2], Medinilla spec.,[3] and especially the cortex of ligneous Dicotyledons, in which they are mainly derived from secondary sclerosis of parenchymatous cells, as will be more closely described in Chap. XV.

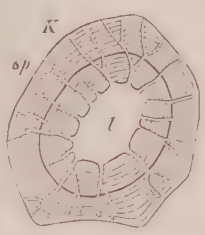

FIG. 52. Transverse section of a short sclerenchymatous (stone) element from the root tuber of Dahlia variabilis. *l* lumen, *sp* pit-canals, *K* spot, by which an inner system of layers is separated (mod.). From Sachs' Textbook.

Transitional forms to the sclerenchymatous fibres are supplied by the rod-shaped stone-elements of many cortical layers, the short pointed fibres of the Cinchoneæ, the short and pointed branched stone-elements of the cortex of Firs and Larches, &c.

In the Monocotyledons the elements of this category are rare; but we must include under this head the multiseriate dense layers beneath the epidermis of stems of Palms[4], and elements with large cavity, and large pits, which form in the cortex of the root of many Aroids (e. g. Tornelia fragrans) 3–4 layers of cells outside the endodermal sheath of the vascular bundle, and in Raphidophora angustifolia[5] also in the inner cortex of the stem a ring of 1–2 layers in thickness.

Typical stone-elements are wanting in the Cryptogams.

(*b*) A second form of short sclerenchyma is represented by the peculiar *covering plates* which Mettenius[6] first distinguished in species of Trichomanes under the name

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[1] Hooker, Trans. Linn. Soc. vol. XXII.—Graf Solms-Laubach, in Pringsheim's Jahrb. VI. p. 530.—Eichler, Balanophoreæ Brasilienses, Tab. II.

[2] Mohl, Ranken- und Schling-pflanzen, p. 89.—Ibid. Poren d. Pflanzenzellgewebes, p. 32.

[3] A. Gris, Ann. Sci. Nat. 5 sér. XIV. p. 50.

[4] Mohl, Palmarum structura, pag. VI. Tab. A. C. Verm. Schriften, p. 136. — Botan. Zeitg. 1871, Taf. II.

[5] Van Tieghem, Struct. des Aroidées, *l. c.*

[6] Hymenophylleen, *l. c.* p. 418.

Stegmata, and which, as shown by later investigations of Rosanoff[1], occur not unfrequently among the Monocotyledons also. They always appear on the outer surface of sclerenchymatous or sclerotic bands of fibres (either such as pursue a separate course, or accompany vascular bundles), and are applied to these in longitudinal rows, which by the arrangement of their elements lead us to conclude that they arose by transverse division of spindle-shaped cells. The single elements are small, and have the form of flat, or (in the Monocotyledons) plano-convex, usually rectangular plates, with the flat side contiguous with the fibrous band. As regards their structure they are characterised by unequal thickening on different sides, usually also by partial silicification of their walls; they vary extremely in individual cases according to the species or systematic group. In the species of Trichomanes, the wall is strongly thickened on one side, i. e. on the inner face, which is contiguous with the fibrous band. In some few species the thickening is uniform on this surface; it is equally rare to find it so arranged that it occupies the periphery of the inner wall in a ring-like manner. Usually there rises from the middle of the inner wall into the cavity a cushion-like protuberance, hollowed in the middle, or comb-like bands placed symmetrically near the middle. On the varying special forms of these outgrowths, compare *l. c.* Those outgrowths protruding inwards and the region immediately surrounding them are distinguished from the rest of the wall, which shows the cellulose reaction, by their granular appearance and strong silicification.

Similar covering plates, perhaps more properly included under the crystal-containing structures, since each contains an aggregation of calcium oxalate, occur, according to a short statement by Mettenius, in certain of the Cyatheaceæ.

The fibrous bands in the stems, leaves, and roots of Orchideæ (Pholidota, Stanhopea, &c.[2]), Palms (Chamærops, Phœnix, Caryota, &c.), of Maranta compressa, Arundinaria spathiflora, have interrupted longitudinal rows of plano-convex stegmata on their exterior. The convex outer wall of these is thin, the inner thickened to a half-spherical rough body, which almost fills the cavity, and consists mostly of compounds of silicon. Often 2–3 such silicified bodies occur in place of one. (Rosanoff found similar silicified bodies also in cells containing chlorophyll and starch on the fibrous bands in the margin of the leaf of Galipea macrophylla, one of the family of Diosmeæ.) The fibrous bands in the lamina of the leaf of Scitamineæ (species of Maranta, Heliconia, Thalia) show small stegmata, the structure of which seems to differ from that just described, and remains to be investigated.

Sect. 30. **Sclerenchymatous fibres**, of elongated spindle-like shape, with sharp ends, simple or branched, are the form of strengthening tissue which is universal, especially in Phanerogams; they are sometimes in uninterrupted lateral connection, and united, with pectinated[3] ends, into bundles and sheaths; sometimes they are imbedded singly in other tissues.

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[1] Botan. Zeitg. 1871, p. 749.

[2] Compare Link, Botan. Zeitg. 1849, p. 750.

[3] [It is believed that this translation will convey the meaning intended by the use of the word 'verschränkt,' the idea being that of an arrangement similar to the fingers of two folded hands, or of two combs (*pecten*) with the teeth of the one passing between those of the other. The word *pectinatory* will be used subsequently in describing the course of the vascular bundles (Chap. VIII, A).]

The fibres in question are frequently called also *Bast-fibres*, or *Bast-cells*, after a region in which they occur especially often in the Dicotyledons, and, in connection with these terms, Sanio has called those fibres which occur in the secondary xylem, and which belong also in part to this category, bast-fibre-like, or *libriform* fibres. Comp. Chap. XIV. P. Moldenhawer[1] calls them fibrous tubes.

The name bast, or liber, is at present used for two quite different things. Originally it was used as a topographic anatomical term, for a definite region of the cortex of the Dicotyledonous stem, which is, it is true, as much characterised by definite forms of tissue occurring in it as by its position (comp. Chap. XV). Among these forms of tissue sclerenchymatous fibres are quite generally characteristic; they are present indeed in many cases in very large quantity, and are very conspicuous as compared with the other tissues. On the latter ground, and since the really characteristic structure of this cortical region was not known, they were considered as the essential tissue of the bast-region, and the name bast was transferred from the region to the sort of tissue, but later again used for both without sharp distinction. Since the sort of tissue is by no means limited to this region, the result was that bast was found at other places than in the bast, or that there is bast without bast, in other words that doubt and controversy arose. Now it is in itself indifferent which meaning is attached to the name, and grounds may be brought forward for authorising both the above uses of it, but it certainly cannot be used for two quite different ideas. In the choice to be made accordingly it seems to me decisive that the topographic meaning of the word is the older, and has always been the more usual. Its use will therefore be here limited to the region to be treated of later, and the fibres in question will therefore be called *Bast-fibres*, wherever they belong to this region.

The form of the sclerenchymatous fibres varies within the above stated limits according to species and part. Their transverse section is acutely angular, where they are closely united into bundles; it is round in such fibres as lie single and loose in intercellular spaces, as in many leathery leaves, in the foliage of many Aroideæ, &c. Those firmly connected into bundles are as a rule *simple*, i.e. unbranched, spindle-shaped, usually with continued and gradual decrease of transverse section towards the ends, while the much-elongated forms are usually drawn out at the ends into extremely fine points. This form—subject it is true to many exceptions—is the rule also for the fibres occurring in longitudinally elongated parts, but not closely connected into bundles: for instance, for most of the fibres, and even the isolated bast-fibres, which are scattered in the parenchyma of the roots of many palms (Chamædorea elegans), the petioles and pinnæ of Cycadeæ[2], &c. A remarkable peculiarity of form is shown by the very long bast-fibres of many Apocyneæ, and Asclepiadeæ (Nerium, Vinca, Asclepias spec.), since they are in their longitudinal course alternately narrowly constricted, and then again suddenly distended; the same is the case, in rather irregular form, in the bast-fibres of species of Sida, Urena, and the species of Corchorus which yield Jute[3].

Even the spindle-shaped fibres, which have just been mentioned as being usually simple, show not uncommonly, when isolated, shortly- and unequally-branched ends, or here and there at other points a branch usually of insignificant size.

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[1] Beitr. pp. 11–61. [2] Moldenhawer, Beitr. p. 34.
[3] S. Wiesner, Microskop. Unters. p. 24 ff., and Idem, Rohstoffe, cap. 11.

On the other hand there commonly occur in Phanerogams fibres which are freely and often abundantly *branched*, and of a form which varies according to the special place of their occurrence: these usually occur in dissimilar lacunar tissue, with their branches projecting or pushed into its interstices. Inasmuch as these project like many branched hairs into wide, air-containing spaces, as in the Nymphæaceæ, Limnanthemum, Aroideæ, Rhizophora, the description of them will be more clearly given when we treat of these spaces (Sect. 53), and we need only draw attention here to their connection with the tissues treated of in this chapter. They also occur more especially in numerous tough, leathery foliage-leaves, though not in the majority of them; they push their branches into the intercellular spaces of the parenchyma, and appear to serve as strengthening apparatus for that tissue. With reference to the relations of their arrangement, to be treated in Chaps. IX and X, may here be mentioned the short-branched fibres in the leaf-lamina of Proteaceæ (Hakea nitida, ceratophylla, saligna, &c.[1]), the long- and finely-branched fibres in the lamina of Olea europæa, emarginata, fragrans[2], the thick, starlike, short-branched ones of Camellia

FIG. 53.—From a transverse section of the leaf of Camellia japonica. *P* parenchymatous cells, with chlorophyll grains and oil drops; *F* thin vascular bundle; *V* branched sclerenchyma fibre. From Sachs' Textbook.

japonica[3] (Fig. 53), Statice monopetala, the beautiful stellate, many-armed ones in the lamina and petiole of Fagræa obovata, and auriculata[4]. Also the leaf-lamina of the above-named Aroideæ, especially the Monsterineæ, and the Nymphæaceæ, may be here again cited. Stellate-branched fibres occur in the foliage-leaf of Sciadopitys, Dammara, Araucaria imbricata[5]. Long-branched ones, sometimes of huge size, form at least half of the substance of the leaf in Gnetum Gnemon, and G. Thoa.

The relation between breadth and length of the fibres varies greatly both according to species and in different parts of the same species, and in the self-same part and the self-same bundle it often varies within wide limits. This is to be taken

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[1] Meyen, Harlemer Preisschrift, p. 84, Taf. V.—Mohl, Verm. Schr. Taf. VII. fig. 2.—Schleiden, Grundz. 3 Aufl. I. p. 277.

[2] Moldenhawer, Beiträge, p. 61.—Thomas, *l.c.* p. 32.

[3] Kraus, Cycadeen-fiedern, *l.c.* p. 327.

[4] O. Buch, Ueber Sklerenchymzellen. Diss. Breslau, 1872, p. 16.

[5] Thomas, *l.c.* p. 35.—Mohl, Botan. Zeitg. 1871, p. 8.

into account in the statements of average, which require confirmation throughout. The published measurements of simple bast-fibres give for the shortest forms, such as those of Peruvian bark, a relation of about 1 : 10 to 1 : 20; for the longest, found among the Urticaceæ, a length exceeding the greatest breadth two or three thousand times (to 1 : 4000). The branched forms are as a rule relatively short and broad, e. g. Fig. 53, but much-elongated specimens also occur.

As examples we may cite the following few measurements found by Mohl[1] and Wiesner[2], and in the Quinine bark by Vogl[3], for fibres of bast and bundles; for further details we must refer to Wiesner's summary, *l.c.* Where only the length is given, the medium of the measurements of breadth given may serve as the breadth.

	Length. mm.	*Greatest breadth of fibre.* mm.
Species of Cinchona, bast	0·875 — 1·25	0·031 — 0·25.
Tilia, bast	0·99 — 2·65	average 0·015.
Corchorus spec. (Jute), bast	0·8 — 4.1	„ 0·016.
Phormium tenax, leaf	2·7 — 5·65	„ 0·013.
Linum usitatissimum, bast	20 — 40	0·15 — 0·17.
Cannabis sativa	10 & more	0·15 — 0·28.
Boehmeria nivea	up to 220	0·04 — 0·08.
Æsculus Hippocastanum	1·35 — 1·8.	
Bignonia radicans	0·6 — 1·35.	
Bombax pentandrum	2·025 — 2·92.	
Daphne Mezereum	up to 3·375.	
Clematis Vitalba	0·45 — 0·85.	
Bambusa spec.	1·8 — 3·015.	
Cocos botryophora	0·855 — 1·350.	
Lonicera Caprifolium, bast	18·0 — 26·0.	
Asclepias Cornuti	up to 26·0.	
Urtica dioica	up to 77·0.	

The considerable length of many fibres, together with the occurrence of the chambered fibres to be described below, has given rise to the view that a fibre does or may arise by the coalescence of several meristematic cells disposed in a longitudinal series[4]. More exact investigation however can find *à priori* no sound ground for this, and all minute observations have shown that each simple or branched fibre results from the metamorphosis of *one* cell[5].

The wall of the sclerenchymatous fibres is thickened to an extent which differs according to each special case, and usually so that the lumen is greatly reduced (centripetal); the thickening mass is nearly equally thick all round, or in many cases it projects inwards much more strongly at certain points than at others, e. g. bast-

[1] Botan. Zeitg. 1855, p. 876.

[2] Mikroskop. Untersuchungen im Laborat. d. polyt. Inst. Wien; and Rohstoffe, d. Pflanzenreichs, cap. II.

[3] Die Chinarinden des Wiener Grosshandels, &c. 1867.

[4] Meyen, in Wiegmann's Archiv, 1838, I. p. 297.—Schacht, in Berl. Acad. Monatsber. 1856, p. 517: Lehrb. II. p. 567.—Hanstein, Milchsaftgef. p. 45.

[5] Compare Unger, Wachsthum d. Stammes u. Bildg. d. Bastzellen, Wiener Acad. Denkschr. Bd. XVI; Boehm, Wien. Acad. Sitzungsber. Bd. 53; Sanio, Botan. Zeitg. 1860, p. 210. Further, the statements in Chapter VII upon the intercellular fibres of the Aroideæ, and Chapter XIV.

fibres of Corchorus spec., Abelmoschus tetraphyllus, Sida retusa, &c.[1] The thickening mass is either continuous, as for instance in most fibres used in manufacture, according to Wiesner[2], or in many cases provided with narrow pit-canals, which, especially in the fibres associated so as to form bundles, have almost always the form of narrow, rectilinear, longitudinal, or parallel oblique slits like a left-handed screw[3]

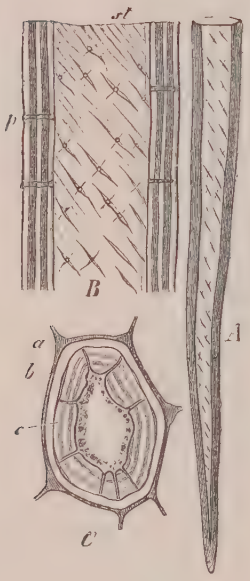

FIG. 54.—Pteris aquilina. *A* half of a brown-walled sclerenchymatous fibre from the stem; *B* piece of one of these more highly magnified (550); *p* profile view of the slit-like pits; *C* transverse section; *a* limiting lamella; *b*, *c* inner layers of the wall. From Sachs' Textbook.

FIG. 55.—Half of a thick sclerenchymatous fibre, with crystals of calcium oxalate imbedded externally in the wall, from the stem of Welwitschia mirabilis. From Sachs' Textbook.

(Fig. 54). Still exceptions to this occur in the short fibres, as the simple ones of the Quinine bark, and the branched ones of the leaf of Camellia: here there are narrow canals, not slit-shaped, but round in section. The sclerenchymatous fibres described by Milde[4] as being spirally thickened, which form a many-layered closed covering on the upper side and on the nerves of the under side of the leaf of Acropteris radiata, would be better described as having slit-like pits. Their membrane, which is thickened till the lumen is almost obliterated, has very numerous, regularly

[1] Compare Wiesner, *l. c.*
[2] Rohstoffe, p. 305.
[3] Mohl, *l. c.* p. 876.—Schwendener, *l. c.* p. 8.
[4] Filices Europæ et Atlantidis, p. 40.

oblique slit-like pits, and these alternate with thick bands of wall of equal height. The epidermal elements overlying this fibrous covering show, as was intimated on p. 71, the same structure.

For the more minute structure of the thickening masses, those general rules hold which apply to the structure of the cell-walls[1]. In the fibres united into bundles, and those in the bast, there may often, but not always, be distinguished three different concentric systems of layers, or sheaths, the outermost limiting layer, an inner layer, and a middle layer, which is usually much broader and softer. The fibres of the Apocyneæ and Asclepiadeæ are excellent examples of the striation and areolation of the wall.—The branched fibres in the leaf of Sciadopitys, Dammara, Araucaria imbricata, Nymphæaceæ, and especially the colossal spindle-fibres made known by Hooker[2], which lie scattered in all parts of Welwitschia mirabilis, are characterised by numerous crystals of calcium oxalate which are imbedded in the outer layers of their walls, and which, especially in Welwitschia, attain a considerable size (Fig. 55).

The wall of the sclerenchymatous fibres is lignified, to a very variable extent according to the special case: of the bast-fibres used in manufacture, e.g. according to Wiesner, those of Flax, Hemp (light yellow with aniline and sulphuric acid), and of Hibiscus cannabinus turn blue (of different shades) with iodine and sulphuric acid, and with aniline and sulphuric acid not at all or hardly yellow; with the preparation of iodine the fibres of species of Corchorus, Sida retusa, Urena sinuata, &c. turn yellow or brown, with aniline and sulphuric acid yellow. In the Ferns and Rhizocarpeæ the fibres of this category have also the above-mentioned (p. 121) characteristic dark-brown colour. In fibres in the bast Sanio[3] often found the especially thick inner layer of the wall cartilaginous and gelatinous, and that it swelled in water, and turned violet with Schultze's solution or solution of iodine in potassium iodide (e.g. in Cytisus Laburnum, Morus alba, Ulmus suberosa, Celtis australis, Ficus Sycomorus, Robinia pseudacacia, Gleditschia triacanthos, Quercus pedunculata, Passiflora suberosa); this phenomenon also occurs in various modifications in the fibrous elements of the secondary wood of Dicotyledons, and will be described with the other properties of these elements in Chap. XIV. Conversely it sometimes happens that sclerenchymatous fibres develope from originally collenchymatous cells, in which case the inner layers of the walls become hard and lignified, while the outer retain the original collenchymatous character: e.g. in the bands accompanying the vascular bundles of Eryngium planum, and Astragalus falcatus[4].

As regards the contents of the fibres we must refer to what was above stated (p. 126) for the sclerenchyma generally. The granular constituents or remnants of the contents, enclosed by many fibres with a larger cavity, e.g. the enlarged parts of those of the Asclepiadeæ and Apocyneæ, have repeatedly led to the view that the bast-fibres contain the characteristic *latex*, which exudes on cut surfaces in the Asclepiadeæ, Euphorbiaceæ, &c., a false idea, which will be discussed in Chap. VI.

In the majority of cases, and in all those which have been hitherto noticed, the

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[1] See Hofmeister, Pflanzenzelle, § 27, 28.
[2] Trans. Linnæan Society, vol. XXIV ('Spicular cells').
[3] Botan. Zeitg. 1863, p. 105.—Ibid. 1860, Taf. VI. 15 and 16.
[4] Schwendener, *l.c.* p. 5.

cavity of the fibres is a continuous hollow, though it is very narrow, and often ceases far from the pointed ends. In the narrow contractions in the Asclepiadeæ and Apocyneæ it may, it is true, be doubted whether it is not sometimes completely interrupted by the thickening of the walls. But on the other hand chambered fibres are often to be found, i.e. such as are cut up into segments or chambers by relatively thin transverse walls continuous with the inner layers of the lateral walls: e.g. in the bast of Æsculus Hippocastanum, in the cortex of roots of Palms, as Chamædorea elegans. Also the chambered fibres in the bast of Vitis, Platanus, Pelargonium roseum, Tamarix gallica[1], in the cortex of Aristolochia Sipho, &c., which contain starch for a time, should perhaps be connected with the above, as cases in which the functions of the cell slowly disappear; the same may be said of the fibres produced from collenchyma, which are common in the cortex of stems.

The chambered elements of the secondary wood of the Dicotyledons, which are also connected with the above, will be spoken of in Chap. XIV.

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[1] Compare Sanio, Ueber die im Winter Stärke führenden Zellen, &c. (Halle, 1858), p. 12; Botan. Zeitg. 1863, p. 111.

CHAPTER III.

SECRETORY RESERVOIRS.

Sect. 31. Bodies of a nature similar to the secretions of the dermal glands (Sect. 19), such as mucilage, and gum, resin, ethereal oils, and mixtures of these designated balsam, milky emulsions of the bodies of both categories which are known in the dry state as 'Gum-resins,' are often found laid by in the interior of the tissues; they occur on the one hand in special *Sacs*, which develope during the differentiation of tissues from definite cells of the meristem: these, retaining their membrane, and growing considerably, are filled completely with the bodies in question, and thereby lose their original cell-nature; or they are found in special *Intercellular spaces*.

There occur in many plants other sacs, arranged similarly to the above, which also arise with the first differentiation of tissue from cells of the meristem, and contain as their sole or preponderating contents crystals of oxalate of lime. All these places of secretion or reservoirs are closely related to one another. The aggregations of crystals are often associated with large deposits of mucilage in the cavity of a sac, so that one may speak of mucilage-sacs with crystals (e.g. tubers of orchids) or of crystal-sacs with mucilage (e.g. Raphide-bearing sacs), according to the preponderance of one or the other body.

As already stated, resin and mucilage often occur mixed together. The form of the sacs merges not uncommonly into that of intercellular spaces filled with the secretory mass, since rows or groups of the former, by absorption of their walls, coalesce to an amorphous intercellular mass. Further, sacs and intercellular spaces with like contents often mutually replace each other, since, in the first place, the same body in different members of the same plant sometimes fills sacs, at other times intercellular spaces, e.g. the red resin of species of Lysimachia and Myrsine; or secondly, of closely allied plants some have sacs, others intercellular spaces filled with the same secretion, at the same points. Examples of this will be found below, among the Coniferæ, Compositæ, &c. Finally, in families more remote from one another, there occurs only one or the other form of secretion and of the reservoir containing it.

The mode of formation of the secretion in the interstitial dermal-glands corresponds closely with that of the schizogenetic resin-passages, which are to be described below. We must here refer especially to the depressed glands of Psoralea.

In consideration of its known properties, calcium oxalate can only be regarded as a body, which is removed from the metastasis of the plant, and is secreted or

excreted. Direct observation teaches us the same of the mucilage, resins, and ethereal oils of the dermal-glands. The fact is no less evident that the resins, mucilages, &c., which are laid by in circumscribed reservoirs, e.g. in the resin-sacs of the Laurineæ, Piperaceæ, Zingiberaceæ, &c., after they begin to be secreted in the meristem, remain, like the calcium oxalate, laid by without further use.

In accordance with all these facts we are bound to regard the whole series of the bodies in question, like the secretions of the dermal-glands, as bodies excluded from the constructive metastasis, and to term them, together with these, *Secretions*. Their occurrence as admixtures of the contents, or as constituents of the membrane of active cells, which may be proved for all bodies of this category, is no argument against this generalisation, since on the one hand calcium oxalate shows plainly that one and the same body may be excreted both in small quantity in an assimilating cell, and in large mass in a special reservoir; on the other hand, in the uncertainty of our present knowledge, a fundamental difference is always possible between what is in the one and in the other case termed, for instance, resin. And finally, this view does not affect that of the application of the secretion to some further uses by the plant, as, for instance, in the well-known case of the hairs on buds.

On these grounds we group the whole of the above-described reservoirs together as *secretory-reservoirs*. There may be distinguished reservoirs of crystals, mucilage, resin, &c., according to their exclusive or preponderating contents. Since resin and ethereal oil occur usually as mixtures, and rarely separate, and since we cannot here enter upon chemical details, which are often uncertain, we shall in the sequel use the words reservoirs of resin, oil, and balsam without claim to exact indication of contents, and usually in connection with the meaning customary for each special case. The term gum-resin is used to indicate, but with still smaller claim to accuracy, the mixture of watery and resinous secretions, which is milky when fresh. According to their structure the reservoirs may be distinguished as *Sacs*, i.e. structures derived from cells, which retain their walls, and are therefore usually termed cells; and *intercellular cavities*, which according to their form are termed either passages or *gaps*. For many of these forms, which vary in structure and contents, the term glands, or *internal glands*, is in use. It will be difficult to banish it, since it has established itself in the incorrigible terminology of Systematic Botany, although, as the sequel will show, it is not at all wanted. If it is to be retained, it ought accurately to be used for all secretory-reservoirs, any other use of it is purely arbitrary and conventional.

With those which certainly belong to this category, we must connect many doubtful structures, such as many 'tannin sacs,' the 'vesicular vessels' of the species of Leek, and others to be named below: this classification may be corrected when more exact observations have been made.

We have already drawn attention to the alternative occurrence of the different forms of secretory reservoirs, in different members of the same plant, or in different genera, or larger circles of affinity.

Similar alternative relations occur here and there between reservoirs and laticiferous tubes (comp. Chap. VI). Even if one discounts the Aroideæ and Musaceæ, the laticiferous tubes of which should perhaps be enumerated in the present chapter, the fact is certain that internal secretory reservoirs are absent from all plants which

are provided with laticiferous tubes. In the group of Artocarpeæ, which in common with the majority of its allies is provided with laticiferous tubes, these are absent, according to Trécul, in Conocephalus naucleiflorus, while in their place this plant has mucilage-containing sacs and cavities. Among those Compositæ, which have been investigated, the Cichoraceæ are distinguished from the rest by their having laticiferous tubes, and by the absence of the oil-ducts present in the others: only in Scolymus are both organs developed.

Further, it is often impossible to ignore an alternative relation between the occurrence of dermal-glands and internal secretory-reservoirs. In the Cycadeæ, Coniferæ, Lauraceæ, Umbelliferæ, Aurantiaceæ, and Clusiaceæ, which have specially large numbers of the latter structures, dermal-glands are absent or rare. For other families, e.g. the Labiatæ, the converse holds. Exceptions, with both sorts of organs side by side, occur not uncommonly it is true, e.g. Dictamnus, and many Compositæ with glandular hairs and internal reservoirs. And finally, we must not omit to notice that both organs may be altogether absent, as e.g. in the Gramina, Cyperaceæ, Palms, many Cruciferæ, Ranunculaceæ, in Taxus alone of the Coniferæ, &c. &c.

The relations, above brought into prominence, between the different organs which form secretions, should always be kept in view during their consideration, in which the first duty is to separate them according to their structure: we will therefore occupy ourselves first with the *sacs* containing secretions. The intercellular reservoirs will be treated of in Chap. VII, and the intermediate structures will be noticed in a fitting place.

1. *Sacs containing Crystals.*

Sect. 32. It is known that crystals of calcium oxalate are generally distributed as constituents of the cell contents. In certain sacs they almost exclusively fill the internal space, and these may be distinguished as crystal-bearing sacs. The crystals[1] consist, as far as is known, entirely of calcium oxalate, which is crystallised either in the quadratic or klinorhombic system—according to Souchay and Lenssen, when quickly deposited it takes the klinorhombic form, with the composition

$$\left.\begin{matrix}\mathrm{Ca\,O}\\ \mathrm{Ca\,O}\end{matrix}\right\} \mathrm{C_4O_6} + 2\,\mathrm{H_2O},$$

when the crystallisation is slower it forms as quadratoctahedra of the composition

$$\left.\begin{matrix}\mathrm{Ca\,O}\\ \mathrm{Ca\,O}\end{matrix}\right\} \mathrm{C_4O_6} + 6\,\mathrm{H_2O}.$$

The fundamental form of the crystals belonging to the quadratic system is the quadratoctahedron, that of the klinorhombic crystals, which are far commoner in plants, is the hendyohedron: derived forms occur of the most various shape, e.g. klinorhombic columns, klinorhombic plates, twin forms, and blunting of corners. As specially common forms, which can hardly be accurately defined crystallographically, may be named the spear- or needle-shaped crystals, elongated and pointed at both ends, which De Candolle[2] has termed *Raphides*. They belong most probably,

[1] See Holzner, Flora, 1864, pp. 273 and 556.—Ibid. 1866, p. 413.

[2] Organographie végétale, I. p. 126 (ῥαφίς = needle).

according to Holzner, to the klinorhombic system. Besides these different, singly developed crystals, there often occur others imperfectly developed, and grown together to angular or stellate *groups*, which, according to Holzner, may belong as well to one system as to the other. The form and system of crystallisation is indefinite in the case of the quite small crystals, which often occur, and appear more like small granules: on these sharp angles and edges may be recognised with a high power.

In the sacs the fully developed klinorhombic forms and the groups almost always occur singly, rarely two together, and fill the greater part of the cell: the Raphides appear always in larger number; as a rule they are nearly equally long and parallel and are closely packed in the sac in a bundle, so that all the ends in the same direction are in one plane; more rarely they vary in length and direction, as in the cortex of many species of Aloe, e.g. Aloe arborescens, in the parenchyma of Mirabilis, and the very small Raphides in the numerous crystal-sacs of the Cinnamon-bark of Ceylon. Here the minute granule-like crystals in an innumerable multitude fill the sac completely, so that in transmitted light it appears to have quite black, densely granular contents: the same occurs in the herbaceous parts of many Solaneæ[1], of Amarantus retroflexus, caudatus, and allies, Sedum ternatum, in the pith and cortex of Sambucus nigra, the cortex of Betula verrucosa, Alnus glutinosa, Staphylea pinnata[2], and the bark of the officinal species of Cinchona[3].

The form of the crystal-bearing sacs is closely related to that of the crystals contained in them, when the latter attain considerable size; but it cannot at present be definitely stated whether the form of the crystal is dependent upon that of the sac, or the converse. The iso-diametric grouped crystals are contained in sacs resembling them in shape, the shorter or longer klinorhombic forms fill sacs of corresponding shape, which are even of very much elongated prismatic or spindle form, e.g. in the rhizome and leaf of species of Iris[4], and in the leaf of Aloe Africana. The sacs containing raphides are elongated in the same direction as the bundle of raphides where the raphides are very large, as in the cortex of Aloe arborescens, in the bulb of Scilla maritima they often attain a great length, in the latter case more than 5^{mm} [5].

These phenomena appear very striking in the bast-bundles of dicotyledonous plants, the tissue-elements of which are derived from elongated spindle-shaped cambial cells. The crystal-bearing sacs arise in this case by transverse division of a cambial cell (Chap. XIV); in those of Guajacum, and Quillaja, which contain a single elongated klinorhombic crystal, few divisions occur: each of the products of this process (? all of them) becomes one crystal-bearing sac. Also it often happens in plants with small solitary crystals or groups of crystals, that only single products of transverse division may develope to crystal-bearing structures. But in very many ligneous plants one cambial cell divides by transverse walls into numerous chambers (20–30), which are hardly or not at all higher than broad, and each of these is filled by a crystal or a group. The general outline of the original cambial cell is meanwhile

[1] Corda, Beitr. z. Kunde d. Kartoffel, &c., in Hlubeck's Œcon. Neuigkeiten, 1847, Nos. 58–60.
[2] Sanio, Monatsbr. d. Berliner Academie, April, 1857.
[3] Flückiger, Pharmacognosie, p. 365.
[4] Unger, Anat. und Physiol. p. 123.
[5] Flückiger, Pharmacognosie, p. 187.

retained, while the whole series of chambers may be isolated, remaining still connected together like a chambered fibre[1]. Hartig has called these chambered or septate sacs, crystal-bearing fibres (Krystallfasern).—Similar phenomena occur also in many woods, e.g. Herminiera Elaphroxylon, and on the outer surface of vascular and fibrous bundles. The stegmata of Mettenius on the brown fibrous-bands of Cyatheaceæ (comp. p. 128) may perhaps belong more properly to this category.

Sacs with very small and numerous crystals, as those of Solanum, Sambucus, &c., usually differ but slightly in form and size from the surrounding cells.

As regards the structure of the crystal-bearing sacs, the bundles of Raphides lie at first within a protoplasmic utricle: in all, or at least in all carefully investigated cases, they are enclosed, when mature, by a rather thick layer of homogeneous, transparent mucilage, which is in its turn surrounded by the slightly thickened cellulose wall: the mucilage reacts, in a few investigated cases[2], similarly to gum arabic, it swells quickly in water, and disappears (dissolves?). It remains to be investigated how far this mucilage belongs originally to the membrane or to the contents of the cell; according to Frank's statements respecting the mucilaginous sacs, containing a small bundle of Raphides, in the tubers of Orchis, the latter is probable. The presence of the mucilage is the cause of the quick swelling of the raphide-bearing sacs in water: their membrane bursts, and the Raphides escape with the swelling mucilage, and scatter themselves through the water. In the elongated or spindle-shaped raphide-bearing sacs, which are common, e.g. in the Aroideæ, the bursting and escape of the needles usually occurs, as Turpin[3] has thoroughly described, at one or at both ends. Hanstein's[4] raphide-containing sac-vessels (vesicular vessels, 'Schlauchgefässe') are mucilaginous raphide-bearing sacs arranged one above another in long longitudinal rows.

These series of sacs occur in large quantity in the parenchyma of many Monocotyledons, stem and leaves of Commelineæ, Palm stems, e. g. Chamædorea: Hanstein found them of large size in the foliage, stems, leaves, and bulb-scales of many Amaryllideæ, of the genera Amaryllis, Sprekelia, Crinum, Pancratium, Eucharis, Alœstrmeria, Narcissus, Leucojum, and Galanthus. In these cases they are found 1–2 layers of cells below the epidermis, and especially in the parenchyma of the lower (outer) side of the leaf. In the Liliaceæ they are less common: they are strongly developed in the leaves of Hyacinthus orientalis, and also in Agapanthus (compare Hanstein, *l. c.*). In the foliage leaves of Scilla, Ornithogalum, Muscari, there are short series, and isolated sacs, and in the scales of the bulbs of these plants only isolated ones.

The stems of Commelineæ are best fitted for the investigation of the series of sacs in question. In the growing internodes of these plants, both in the parenchyma of the cortex and of the middle of the stem, there may be observed single longitudinal rows of cells, each of which is loosely filled with a bundle of parallel raphides. The cells are at first

[1] Compare Sanio, Monatsbr. d. Berlin. Acad. 1857, p. 261; for further particulars see below, Chapter XIV.

[2] Hilgers, in Pringsheim's Jahrb. VI. p. 286.

[3] Sur les biforines, Ann. Sci. Nat. 2 sér. tom. VI. p. 5.

[4] Ueber ein System schlauchartiger Gefässe, etc. Monatsber. Berlin. Acad. 1859, p. 705.—Die Milchsaftgefässe, p. 33.

cylindrical. As the internode extends, the length of the cells and of the raphides increases, till in the case of the cells it exceeds their breadth on an average 3–4 times. Hitherto a thin protoplasmic layer, with a nucleus of sharp contour, lines the delicate cellulose wall. As the internode extends further, the cells which remain thin-walled, become 10–20 times longer than they are broad, the protoplasmic parts disappear, while round the bundle of raphides there is seen only transparent mucilage, which shrinks greatly but without turning misty in alcohol, swells quickly in water till it is unrecognisable, turns yellow with Schultze's solution, and is not dissolved in potash. Meanwhile the raphides do not increase perceptibly in number or size, they form henceforth a relatively small group in the sac filled with hyaline mucilage. According to Hanstein the members of such a series of sacs coalesce, at least frequently and partially, to continuous long tubes, by the breaking down of the transverse cellulose walls which separate them. But the observations cited in evidence of this are not sufficient to substantiate it. It is true it is often found in longitudinal sections that the raphides are irregularly displaced, and have bored through the delicate transverse walls of the series of sacs; but on the other hand sacs are also found closed at both ends, and dense bundles of raphides in them. And one can often directly see the displacement of the raphides and the perforation of the transverse walls in progress before one's eyes. The action of water produces this result, the mucilage swells in fundamentally the same way as in solitary raphide-containing sacs. I could not prove to myself the occurrence of spontaneous perforation of the transverse walls, that is of a coalescence of the series to a continuous tube or 'Vessel.' Where I found a perforation already present, it was a gaping rent, such as is seen to be formed when the wall bursts. Further, it is not impossible to suppose that even in the living plant, when too much water is present, walls may burst, and so the same phenomena appear as are seen in sections. According to all these data, which coincide in the main with the statements of Hanstein, the structures in question may be regarded as nothing more than a special kind of raphide-containing sac distinguished by form and arrangement.

Rosanoff[1] was the first to find in the pith of Kerria japonica, Ricinus communis, in the sacs which accompany the vascular bundles of the petiole of Aroideæ (e. g. Anthurium rubricaule, Selloum, Pothos argyrea, Philodendron Sellowianum), as well as in the parts of the flower of Encephalartos and Nelumbium, that *groups of crystals* are connected with the membrane; either their apices are in close contact with the lateral wall, or they are suspended by bars of cellulose, which extend from the wall into the cavity, as far as single points of the group; these bars are often branched, and often hollowed like tubes. De La Rue found a similar attachment in the parenchyma of the leaf of Hoya carnosa in the case of small groups of crystals, contained in cells which have protoplasm and even chlorophyll (these, however, in the strict sense do not belong to this category), and also in the leaf and petiole of Aroideæ (Pothos crassinervis, &c.). Further, Pfitzer[2], following up an older observation of Schacht[3], showed that the large *solitary klinorhombic crystals* contained in the foliage of Citrus, and those in the cortex of Salix aurita, Populus italica, Celtis australis, Fagus sylvatica, Rhamnus Frangula, Acer opulifolium, and Platanus orientalis, are closely surrounded by a cellulose skin, a large part of the surface of which is attached to the cellulose wall of the sac: this skin arises from the protoplasm of the young crystal-bearing cell, which surrounds the crystal: at first it lies free, later it becomes firmly attached to the cell wall. At the point of contact the lateral

[1] Botan. Zeitg. 1865, p. 329.—Ibid. 1867, p. 41.—Compare also De la Rue, ibid. 1869, p. 537.
[2] Flora, 1872, p. 95, Taf. III.
[3] Abhandl. Senkenberg. Gesellsch. z. Frankfurt a M. I. p. 150, Taf. VII. fig. 21.

wall of the sac is often strongly thickened, especially in Citrus, where the crystal appears inserted in the very thick lateral wall, or in a conical excrescence of it. In the septate sacs of the wood of Herminiera elaphroxylon[1] there lies in each of the almost cubical segments one klinorhombic plate, with one side fitted into the strongly thickened inner wall of the sac, while the rest almost fills the cavity of the segment. I could not in this case find a membrane surrounding the crystal. The space not occupied by the crystal in all these sacs is in the mature state apparently filled with water.

Many crystals of whatever form, with the exception of Raphides, appear to lie free within the membrane of the sac, being either closely surrounded by it, but without attachment, or suspended in an apparently watery fluid. Thus, e. g. the large crystals of Iris, and the crystalline granules. For all these cases, however, it remains to be more definitely determined whether a gelatinous coat or an attachment to the wall is present or not. The general occurrence of such a condition is attested by Payen in his statements on the occurrence of silicious coats round grouped crystals, and of membranous sheathing layers of a granular substance which turns brown with iodine. Compare Hofmeister, Pflanzenzelle, p. 393.

Crystal-containing sacs occur in all parts, and in all tissues of plants; they appear most abundantly, and often in very great quantity [the stem of Cereus senilis contains in the dry substance more than eighty-five per cent. of calcium oxalate (Schleiden)], in the parenchyma of sappy foliage, and in leathery leaves, bordering closely on the vascular bundles, and arranged in rows which follow these, in the bast and pith of dicotyledonous plants, often also in the secondary xylem-parenchyma (Pterocar us santalinus, Hæmatoxylon, &c.), and in the medullary rays of the wood (e. g. Camellia japonica, Vitis; compare Chapter XIV): where large air-containing intercellular spaces are present they are often particularly numerous at the limits of these, and project into them: e. g. Aroideæ, Pistia, Myriophyllum.

They occur in most families, and usually in all genera and species of a family: in those in which regular crystal-bearing sacs are rare, or absent, the calcium oxalate is often deposited in the form of small crystals in the contents of parenchymatous cells, or, as in the Cupressineæ, Taxineæ, Ephedra, and Welwitschia[2], in the cell-membranes.

The more generally this rule applies the more worthy of attention is a series of exceptions. In the Equiseta no oxalate of lime is observed anatomically. The same is the case in most Ferns, Gramineæ, and the Potameæ (with the exception in the Phanerogams of the parts of the flower). Still exceptions occur in many of the above families: such as crystals in the Epidermal cells of Asplenium Nidus, in the covering plates of the Cyatheaceæ (comp. p. 128), numerous clusters of crystals in the parenchyma of the stem of Panicum turgidum.

On the other hand, crystal-containing sacs, or crystals, are not found at all in certain species or genera of families, the members of which, as a rule, contain them in large quantity. In Nicandra physaloides and Petunia nyctaginiflora I found no crystal-containing sacs, while the rest of the Solanaceæ, which have been in-

[1] Hallier (Botan. Zeitg. 1864, Taf, III) gives the outline of these cells correctly, but with a wrong description.

[2] Compare Graf zu Solms-Laubach, Botan. Zeitg. 1871.

vestigated, have them in abundance. According to Gulliver, crystal-containing sacs are wanting in Tulipa silvestris, Fritillaria Meleagris, Lilium Martagon, candidum, aurantium, whilst most other Liliaceæ have them in plenty: Sparganium has many Raphides, the species of Typha have no crystals. Among the Lemnaceæ[1], no Wolffia has crystals; the Lemnæ and Spirodelæ have numerous raphide-bearing sacs, the latter having also many clusters of crystals.

The form of the crystal-bearing sacs, and of the crystals within them, is characteristic for many divisions, families, and species[2]; still general and absolute rules cannot be laid down. In most families of Monocotyledons Raphides occur exclusively, or they preponderate largely, and often occur in vast quantity, e. g. Liliaceæ, Orchidaceæ, Bromeliaceæ, &c. But in species of Allium there are no Raphides, and, as far as is known, crystal-containing sacs are entirely absent. Instead of these there lies in the middle of each cell of the subepidermal parenchyma, on the outer side of the young scales of the bulb, one prismatic crystal, or several grown together[3] (this is specially well seen in A. sativum). In others, e. g. the Araceæ, sacs containing Raphides and clustered crystals occur side by side, often in the same section. In the Iridaceæ only large columnar solitary crystals are to be found. While the Musaceæ have only sacs containing Raphides, there occur in the Marantaceæ and Zingiberaceæ only other forms of crystals. In the Dicotyledons there are most frequently found clustered crystals, or klinorhombic solitary crystals, or both forms together, often also with granular crystals, while Raphides are entirely absent. In certain cases, however, in these plants also the latter occur exclusively or in preponderating quantity. Finally, a few further examples may be added to the above. For further details the reader must be referred to the authors cited, and for the phenomena in the bast of Dicotyledons to Chap. XIV.

Clustered Crystals occur exclusively or greatly preponderate in the foliage of Chenopodiaceæ, Caryophyllaceæ, Cactaceæ, Lythraceæ (Gulliver), and very many other families: and, according to Sanio[4], in the bast of Juglans regia, Rhus typhinum, Viburnum Oxycoccos, V. Lantana, Prunus Padus, Punica granatum, Ptelea trifoliata, Ribes nigrum, Lonicera tatarica.

Solitary klinorhombic crystals in the foliage of Citrus: in the bast of species of Acer, Pomaceæ, of Quillaja Saponaria, Robinia pseudacacia, Virgilia lutea, Melaleuca styphelioides, Ulmus campestris, Guajacum, Berberis vulgaris[5], &c. Also in Abies pectinata.

Sanio found *solitary klinorhombic crystals and clustered crystals* together in the bast of Quercus pedunculata, Celtis australis, Æsculus Hippocastanum, Hamamelis virginiana, Morus alba, Salix cinerea, Fagus sylvatica, in species of Populus, Gleditschia triacanthos, Carpinus Betulus, Ostrya virginica, Corylus Avellana, Tilia parvifolia, Spiræa opulifolia.

Solitary klinorhombic crystals together with clustered crystals, and sacs containing granules, are found in the bast of Betula verrucosa, and Alnus glutinosa (Sanio).

Sacs containing granules alone, in Sambucus nigra.

Raphides are absent in the examples of Dicotyledons hitherto enumerated. They are numerous and preponderate in the leaves of species of Galium and allied genera, in the

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[1] Hegelmaier, Lemnaceæ, p. 33.

[2] For details of the cortex of woody dicotyledons cf. Sanio, *l.c.*; there are very numerous details respecting the leaves in Gulliver, Annals and Magazine of Natural History, vol. XI, XII, XIII, XIV, XV, XVI.

[3] Hanstein, Milchsaftgefässe, p. 36.

[4] Monatsber. d. Berliner Academie, April, 1857.

[5] Compare Sanio, *l.c.*

foliage of Vitis, Cissus, and Ampelopsis: in Vitis they are found in the wood also, and, together with klinorhombic crystals, in the bast, in the cortex of Cinnamomum Zeylanicum, and Olea Europea: in the foliage (leaves and stems) of species of Impatiens, Mesembryanthemum, and Phytolacca, in Nyctagineæ, and Œnothereæ.

It will be seen from what is above stated that here also differences occur in equivalent parts of plants closely allied to one another and of similar habit, and that one cannot designate any form of crystal-containing sacs as a general peculiarity of a family, or as a phenomenon of adaptation. Among the often-quoted Solanaceæ the majority (*e.g.* Solanum tuberosum, Dulcamara, species of Nicotiana, Scopolia atropoides, Jochroma Warczewiczii) have very numerous sacs with granules throughout the parenchyma of the stem (in the leaves often clustered crystals). Jochroma coccineum has granule-containing sacs in large quantity in the parenchyma of the pith, but in the cortex only solitary prismatic crystals: in Atropa Belladonna the granule-containing sacs are entirely wanting in the foliage: it has been above noted that crystal-containing sacs are completely absent in Petunia. All these statements hold for true crystal-containing sacs, and it must always be borne in mind that, besides these, smaller solitary crystals of all forms may occur in the contents or in the membranes of other tissue-elements.

The crystal-containing sacs appear while the tissues are still young, usually when the tissues begin to differentiate[1]; in the leaf of Citrus, according to Pfitzer, their formation begins when it is about 3 ctm. in length: they are developed in greater quantity only in the almost fully unfolded, but still tender leaf, when its cells attain their last definitive extension and thickening of the membranes. They retain unaltered through life that size and structure which they have attained when the differentiation of tissues is complete.

In connection with the crystal-containing sacs must be mentioned the occurrence of cells containing Cystoliths, which are found in the Acanthaceæ, and many Urticaceæ (Pilea), in the epidermis of which they have been described above (p. 105), also scattered in the parenchyma of the cortex, and even of the pith. As regards their structure, all that has above been said of the same structures in the epidermis holds good.

2. *Sacs containing mucilage.*

Sect. 33. When vegetable mucilage and gummy bodies, occurring within the tissues, do not belong to the cell contents of assimilating parenchymatous cells (as is the case with the plentiful mucilage in roots of Borraginaceæ, e. g. Symphytum, Cynoglossum, &c., or that of mucilaginous sappy parenchyma, e. g. in species of Aloe, comp. p. 116), they fill completely or almost entirely the cavity of special mucilage-containing sacs[2]. Such sacs occur in the parenchyma of the Malvaceæ, Tiliaceæ, Sterculiaceæ, in the cortex of the officinal Lauraceæ, the Ulmeæ, the Cactaceæ[3], and of the tubers of Orchis, also in the cortex of the firs (Abies pectinata and its allies). They are in all cases distinguished from the cells of the surrounding parenchyma by their greater size, and are distributed between these either singly, or

[1] Compare Hilgers, *l.c.*

[2] Trécul, l'Institut, 1862, p. 314.—A. B. Frank, Ueber die Anatom. Bedeutung, &c., vegetab. Schleime; Pringsheim's Jahrb. V. p. 161, Taf. XV, XVI.—Idem, Zur Kenntniss d. Pflanzenschleime, Journ. f. pract. Chemie, Bd. 95.

[3] Schleiden, Anatomie d. Cacteen, p. 8, where, by the way, the structure is not rightly represented.

in groups or rows, usually without any clearly recognisable order. In the tubers of Orchis they appear fairly regularly as wide sacs completely filling the meshes of a network, which is composed of plates of starchy parenchymatous cells, one or more layers thick, which face in all directions[1]. When lying in water they appear as intercellular cavities filled with swollen mucilage, and were described as such by the older anatomists[2].

If the swelling of the mucilage be prevented, e. g. by treatment with alcohol, the space enclosed by an outer cellulose membrane appears either entirely filled with the firm mass of mucilage, or partially, so as to leave an unimportant central cavity. The mass of mucilage shows in the majority of cases—Malvaceæ, Cactaceæ[3], Lauraceæ,—the structure of a very thick, abundantly and delicately stratified cell-wall; it often has even pits (Malvaceæ), and is, as regards its origin and morphological significance, nothing more than a cell-wall which has thickened strongly at the expense of the internal cavity. According to Trécul's statements this point may, it is true, be doubted, and new investigations desired. In other cases, and as types of these the tubers of Orchis may be named, the mass of mucilage has no such stratification: it developes from a drop of mucilage, which appears first like a vacuole within the protoplasm, and surrounds a bundle of Raphides lying near to the nucleus: this drop as it grows completely displaces the protoplasm and nucleus, while the bundle of Raphides remains imbedded in the mature mass of mucilage. The sacs in the cortex of the silver-fir appear to correspond to these in structure, their development remains to be more accurately investigated.

In later stages of life the sacs often appear swollen up in the living plant to structureless masses (e. g. in Althæa rosea): these then fill up cavities in the parenchyma of various form and size, according as they have been derived from the swelling of one or several sacs. These latter structures may best be connected with those mucilage-containing cavities, originally derived from a group of swollen mucilaginous cells, which are described in the parenchyma of the Lime (cortex, leaves, bud-scales[4]): also the 'gum'-bearing cells, and cavities formed by the swelling of these, which were described by Trécul[5] in the parenchyma of the branches of Conocephalous naucleiflorus. This author himself doubts whether the gum-cavities of the species of Quiina described by him[6] belong to this category, or to the products of secondary disorganisation. Subject to the same doubt, the small masses of mucilage scattered through the parenchyma of the stem and leaf of Welwitschia[7] may be mentioned here.

The sacs with which we are now dealing may be distinguished from those gummy and mucilaginous products of disorganisation which may be derived in a secondary manner from the most various tissues, by their originating directly from the meristem; they often appear as its first recognisable product of differentiation,

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[1] Frank, *l. c.*—Berg, Atlas z. pharm. Waarenkunde, Taf. 23.
[2] Meyen, Secretionsorgane, p. 22.
[3] Wigand, in Pringsheim's Jahrb. III. p. 149, Taf. VII. 6.
[4] Frank, Beitr. z. Pflanzenphysiologie, p. 113.
[5] Comptes Rendus, tom. LXVI. p. 575 (1868).
[6] Ibid, tom. LXIII. p. 717 (1866).
[7] Compare Hooker, Welwitschia, pp. 11, 19.

differing from the cells of the surrounding parenchyma in their more rapid growth, and in the absence of any formation of even transitory chlorophyll or starch. It is plain that the cases of subsequent swelling of sacs are to a certain extent connected with those of secondary disorganisation. On the other hand, it cannot be denied that these structures are closely related to mucilaginous epidermal cells (p. 73), and sacs containing raphides (p. 139), and to sclerenchymatous elements, e. g. those of the bark of Punica.

3. *Sacs containing resins and gum-resins.*

Sect. 34. Sacs, which from the moment of differentiation of tissues are permanently filled with the above-named bodies, the resin being usually accompanied by ethereal oil, occur as characteristic components of numerous families, or of single genera and species; in the latter case they usually represent at certain places the intercellular reservoirs, which occur in other parts of the same plant (e. g. Tagetes, Lysimachia), comp. Sect. 50.

Taking the extreme cases into account, we may distinguish two forms of these sacs, *short* and *long*. The former are of almost iso-diametric and usually roundish form, and have thin, smooth, homogeneous membranes which, in the cases hitherto investigated (Laurus, Camphora, Acorus Calamus, Zingiberaceæ, Canella), give when mature a yellow instead of a blue coloration with iodine and sulphuric acid, and are not destroyed by strong action of the acid [1]. Protoplasm is apparently absent in the mature sac, which is completely filled by one homogeneous variously-coloured drop of resin, or by an aggregation of several of these. Sacs of this category lie solitary, or in small groups in the parenchyma (primary or secondary), with the cells of which they are strongly contrasted by their highly refractive contents, and are often distinguished by their more considerable size, in the Zingiberaceæ, Acorus, Piperaceæ, Lauraceæ [2], Magnoliaceæ (Magnolia, Drimys, Liriodendron [3],) Canellaceæ, in the cortex of Croton Eleuteria, and its allies (Cascarilla bark), Galipea officinalis (cortex Angusturæ [4]), and Aristolochiaceæ. In the majority of the above groups and genera the sacs in question are the only reservoirs of the characteristic secretions. But Galipea has also, according to the statements of Engler [5], intercellular reservoirs in the primary parenchyma.

In the root of Acorus [6] Calamus and gramineus, the inner of the two superficial layers is composed of regular prismatic resin-sacs. Van Tieghem ascribes a similar structure to the roots of Xanthochymus pictorius, and Rheedia lateriflora, in which the intercellular reservoirs present in the stem and leaf are absent, and are replaced by these sacs (comp. below, Sect. 50). It remains to be investigated whether the hypodermal layer of tissue containing drops of oil and resin, which is described in the roots of Valeriana, belongs to this category [7].

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[1] [Compare Zacharias, Bot. Zeitg. 1879, p. 617.]

[2] Unger, Anatomie und Physiol. p. 210.

[3] Treviranus, Beiträge, figs, 34, 35.

[4] Compare the figures in Berg's Atlas z. Pharm. Waarenkunde, which refer to the above-named barks and other drugs produced from the families above cited.

[5] Studien über d. Rutaceen, &c., Halle, 1874.

[6] Van Tieghem, Struct. des Aroidées, Ann. Sci. Nat. 5 sér. tom VI. p. 175.

[7] Compare Meyen, Secretionsorgane, p. 63, Taf. VI. fig. 22.

In the primary parenchyma of the roots of many Lysimachias and Myrsineæ also, and in the secondary parenchyma of many Compositæ, sacs are found as substitutes for the intercellular reservoirs which are present in other parts of the same plants; their mode of occurrence will be more accurately stated in the subsequent section which deals with these structures.

The development of the short resiniferous sacs, and especially the history of development of their contents, is still uncertain, and requires thorough investigation.

I have termed the other category *long sacs* because they either permeate the tissues as long tubes, which are simple, i. e. arise from one greatly elongated cell, retaining its original wall, and are arranged singly or in longitudinal series, or they form long series, which follow a similar course, though the single members of these are but little elongated. These two special forms may graduate into one another in a single plant (e. g. in the Convolvulaceæ) according to the extension of the members to which they belong.

Most of the long sacs here grouped together have been only partially investigated, or very unequally in their different relations, it is therefore possible that to a certain extent quite heterogeneous structures stand provisionally side by side; the features common to them all are sufficiently indicated by the present treatment of them. The contents of the sacs in question, at least when fully developed, usually consist of a milky mass of resinous bodies (in the widest sense) and watery solutions or mucilage. Their distribution varies in special cases; the rows of sacs in species of Allium and the sacs of the Cinchoneæ permeate the parenchyma alone. But most of these structures accompany the vascular bundles or lie in the secondary bast, being arranged more or less similarly to the laticiferous tubes of various families. In many plants, e. g. certain Aroideæ and Musaceæ (comp. Sect. 47), they occupy exactly the position which is held by the laticiferous tubes in other nearly allied forms, these being absent in the above plants. All this points to a near relationship, both morphological and physiological, with the laticiferous tubes, or at least with certain organs ascribed to this category; many of the sacs in question are hence frequently described as laticiferous tubes. It has at all events been assumed for many of them that they arise, as is the case with articulated laticiferous tubes, by coalescence of longitudinal rows of cells, a view which is generally incorrect. When however the sacs of this category are arranged in a linear series, e. g. in Convolvulaceæ, Acer, Allium, it appears that such coalescence may occur here and there for a short distance by perforation of transverse walls, or even of thin pits on the lateral walls; it is however always difficult to distinguish (and I have not been quite certain in any case) whether the perforations observed are spontaneous, or were formed in the process of preparation.

The organs to be placed in this category are the following: the series of sacs filled with latex in species of *Allium*, and perhaps also of Aloe; those to be described below (Sect. 47) in the *Aroideæ*, and *Musaceæ*; the series of sacs described as 'laticiferous vessels' in the *Convolvulaceæ*: and closely allied to these in structure and arrangement are those of the *Sapotaceæ* (Sideroxylon, Bumelia, Isonandra), those which run along the vascular bundles of many *Cynareæ*, and finally those of *Sambucus*, *Cinchona*, *Ladenbergia*, and *Acer*. It must remain undecided whether the resiniferous

elements in the parenchyma of the secondary wood of Coniferæ belong to this series. (Comp. Chap. XIV.)

As doubtful cases may here be mentioned the sacs filled with pigment, in *Sanguinaria*, *Glaucium*, and *Macleya*, which will be again noticed in Sect. 47; the sacs or cells containing gum-resin which accompany the vascular bundles of species of *Aloe*; lastly, the various 'cells' filled with peculiar pigments (usually watery solutions), such as those in the roots of Rheum[1], Rubia, &c.

The following particulars may be quoted concerning those organs of this series which have been more accurately investigated.

1. Hanstein[2] discovered in those species of **Allium** in which he sought them (A. Cepa, fistulosum, ascalonicum, &c.), large wide sacs, which he grouped with the series of raphide-containing sacs of other Monocotyledons, as sac-like vessels (vesicular vessels). As regards their form and arrangement they closely resemble these latter sacs, e. g. those of the Amaryllidaceæ, though they differ from them in structure, and especially in the character of their contents.

In the scales of the bulb of species of Leek they appear as numerous opaque lines, which are visible to the naked eye, and run longitudinally like nerves. They lie near the outer surface of the scale, between the second and third layers of parenchyma. The single sacs are of circular transverse section, and wider than the cells of the neighbouring parenchyma which abut closely upon them; they are much longer than broad; are often somewhat swollen below their flattened ends, and are arranged in longitudinal series one above another (Fig. 56).

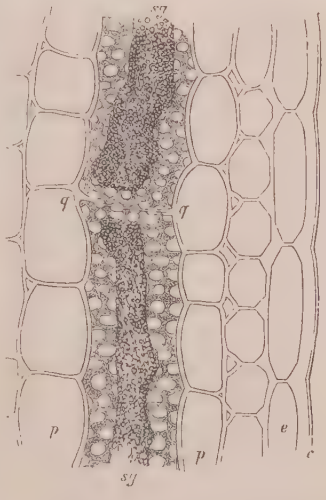

FIG. 56.—Allium Cepa; longitudinal section through a bulb-scale. *e* epidermis, *c* cuticle, *p* parenchyma; between the first and second layers of parenchyma ends of two sacs which abut on one another and are divided by the pitted transverse wall *q*—*q*; they are represented as cut in half longitudinally; *sg* their contents coagulated by potash; the longitudinal wall behind this abuts on another lower sac, and shows accordingly the pitting mentioned in the text. From Sachs' Textbook.

At the base of the scale they are often shorter than above, and not unfrequently bear sac-like branches, which connect neighbouring series with one another as transverse or oblique anastomoses: here also rows of sacs occur in close longitudinal aggregation.

The sacs are filled with a granular cloudy fluid, which appears to the naked eye on the surface of sliced onions as a pale milk, in the sac itself it is cloudy, but still transparent. The nature of the constituents of these contents has not yet been thoroughly investigated: I have not been able to substantiate the obvious conjecture that they especially contain the oil of garlic. Raphides or other crystals are entirely absent. A large, slightly elongated nucleus is still to be found in sacs that are not too old. The walls of the sacs are colourless and delicate, so that in sections they are squeezed in laterally by the turgescent parenchymatous cells: where they touch the latter they are smooth or have solitary small round pits: but over the whole surface where two sacs are in contact with one another the wall is, like a coarse sieve, covered with crowded, round—not perforated—pits, while between these lie rather thick bands of membrane. This is the case both with the transverse walls,

[1] Unger, Anat. p. 206.

[2] *L. c.*, compare p. 139

and with the less common lateral surfaces of contact of sacs which are contiguous longitudinally.

The rows of sacs are continued into the foliage leaves: they have here a similar position and structure to those in the scales of the bulb, but the sacs are much more elongated, and the fluid contents less cloudy. Similar sacs to those of Allium have hitherto been found only in species of Triteleia (Hanstein).

2. The 'Sap cavities' in the leaves of officinal and other species of **Aloe** are of doubtful relationship to the structures under discussion. They accompany the longitudinal vascular bundles in the form of a band of prismatic sacs, which presents in transverse section a semicircular multiseriate appearance: these sacs have flat ends and are arranged one above another in longitudinal rows. The length of one sac varies, according to Trécul's measurements, e. g. in A. vulgaris, from 0·40 mm to 1·30 mm, while the width is considerable, being, in the species above named, as great as 0·10 — 0·13 mm. They are thin-walled, and are filled, according to the species, locality, and time of year, with 'sap' of varying intensity of colour, or even with colourless 'sap' (Aloe arborescens, plicatilis), which is homogeneous, or it contains suspended in it spherical drops, which vary in number, size, and special structure. It has been asserted that by disorganisation of single sacs, cavities are formed in the band, which contain the same 'sap.' It is not improbable that the gum-resin, which is the 'Aloe' of the shops, is derived from these sacs, but even this is not certain. The band is marked off from the surrounding chlorophyll-parenchyma by a layer of apparently prismatic, rather flattened small cells or sacs, which often also contain coloured sap, and in these Flückiger saw, in A. soccotrina, after slow evaporation of the 'clear, tenacious, beautiful yellow contents,' distinct yellow plates (of Aloin?) crystallise out. For further details about these organs, which still require exact investigation, see Unger, Anat. u. Physiol. p. 206; Flückiger, Pharmacognosie, p. 106, and the detailed account of Trécul, Compt. rendus, 1 Mai, 1871; Ann. Sc. Nat. 5 série, t. XIV. p. 80.

Numerous species of Haworthia and Aloe ciliaris have, according to Trécul, no secretory sacs.

3. In the stems of **Sambucus** (S. nigra, S. Ebulus) there occur in the cortex outside the vascular bundles, and especially in the periphery of the pith, longitudinal lines, which turn dark brown on drying, and in this condition have even been regarded as Fungi[1]. According to Dippel's exposition[2], which I find to be confirmed in all essential points, these lines consist of elongated, spindle-shaped sacs of very considerable length and breadth, which are tapered at both ends. The transverse section of these sacs is round, and the breadth varies between 0·025 mm and 0·164 mm (Dippel). It is stated by Dippel that the length of the mature sac usually exceeds 18 — 20 mm: the only one isolated by him without injury was 14 mm in length. They seem to me to reach a considerably higher figure, and even to equal the whole length of an internode, that is to attain a length of 20 cm and more: but it is difficult to decide this for certain, owing to the difficulty of isolating them intact. At all events these lines consisting of sacs, which turn brown on drying, traverse the whole length of the internodes, and even pass through the nodes from one internode into the next. The membrane of the sacs is rather thin and colourless: in older internodes it is thickened and stratified, and has round or oval, non-perforated pits. The contents are, when young, a cloudy, finely granular, rather tenacious mass, which fills the whole cavity. In older stages this mass is often attached, partially or entirely, to the walls, and the central cavity is then filled with an apparently watery fluid: in old parts it assumes an homogeneous, firmly gelatinous character, and

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[1] Compare Oudemans, Over eene bijzondere soort von buizen in den Vlierstam (Sambucus nigra), tot hiertoe voor een fungus (Rhizomorpha parallela Roberge) gehouden. Verslag. k. Acad. von Wetenschappen, Natuurkunde, 2 Reihe, tom. VI. (1872).

[2] Die milchsaftführenden Zellen der Holunderarten. Verhandl. d. Nat. Vereins f. Rheinland u. Westphalen, Jahrg. 22, pp. 1–9, Taf. I (1866).

a red-brown colour. The nature of the material composing this mass is not clear (comp. Oudemans, *l. c.*). According to the reaction with salts of Iron it contains much tannin: it swells in water, alcohol, ether, glycerine, alkalies, acetic acid: it diminishes in volume in mineral acids and salts of metals: the originally colourless mass is coloured by most acids (also by iodine and sulphuric acid), alkalies, and metallic salts (with exception of compounds of iron) a reddish brown, by Schultze's solution it is coloured blue. Carmine and aniline colouring matters are taken up by it in very large quantity.

Each of these peculiar structures originates, as Dippel has shown, from one simple cell, which grows to a great length. The observation of their development in the youngest internodes leads unmistakeably to this view. In the highest internodes of Sambucus nigra tangential longitudinal sections, which include the peripheral zone of pith uninjured, show cells with the above characters of the contents scattered in the parenchyma: these are easily brought into prominence by their deep aniline-staining; they are scattered through the parenchyma: the longest are almost of equal length to the internode, the shortest are hardly twice as long as broad. In more elongated internodes, up to 5 mm long, the first sacs are already considerably lengthened, while new cells, some placed alongside, some above the first, assume the same characters. Such conditions at first sight allow of the assumption that the sacs arise from rows of coalescing cells, but this is confirmed by no direct observation. In older and quite mature sacs the mass of contents is easily divided, especially after the action of potash [1], into cylindrical pieces sharply limited by transparent bands: these resemble cylindrical cells arranged in longitudinal series: but from evidence derived from direct observation of young stages of development they can only be regarded as products of the action of the reagent. Drawings like Fig. 9 of Oudemans, *l. c.*, represent doubtless something else than the development of the sacs.

4. The sacs containing gum-resin or latex which, according to Karsten, occur in all species of the genera **Cinchona** and **Ladenbergia**, appear to be closely allied to those of Sambucus [2]. They are found, like these, partly in the periphery of the pith, partly in the young outer cortex, close to the bast layer. In many species (C. heterophylla, obtusifolia, &c.) they remain small, and are difficult to recognise even in the cortex when two years old. But in other barks, such as those derived from Cinch. scrobiculata, ovata, umbellulifera, &c., they attain a width of 100 μ to over 300 μ, in C. lancifolia (?), according to Vogl, even of 700 μ, and a length of at least several millimetres. As far as I could see they have conical closed ends: Karsten's statement that they arise from the coalescence of longitudinal rows of cells certainly requires further investigation. The sacs have a rather thick wall, which shows cellulose-colouring after treatment with potash. Their contents, which include much tannin, are described as milky in the fresh state; in the dried bark they are so shrivelled that the sacs usually appear empty.

5. A great number of **Cynareæ** [3], and many **Vernoniaceæ**, have in the stem, petiole, and stronger ribs of the leaf on the outer side of the vascular bundles, or of the fibrous band which limits them, a group of sacs filled with a fluid made milky by numerous resinous (?) drops: this exudes on cut surfaces in the form of small white milky drops, and is thus visible to the naked eye. In old sacs the contents coalesce to a very glutinous string. In many species, e. g. Lappa, Cirsium lanceolatum, the sacs are placed not only at the outer, but also at the inner margin of the vascular bundles. The sacs themselves have a spindle-like form; they are closed at both ends, and attain in the mature plant a con-

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[1] Compare Hanstein, *l. c.* p. 21.

[2] Karsten, Die medic. China-Rinden Neu-Granada's. Ges. Beitr. p. 382.—Berg, China-Rinden d. Pharm. Sammlg. zu Berlin.—Idem, Atl. d. Pharm. W. enkunde.—Vogl, China-Rinden d. Wiener Grosshandels.—Flückiger, Pharmacognosie, p. 566.

[3] Trécul, Des vaisseaux propres . . . des Cynarées laiteuses . . . L'Institut, 1862, p. 266.—Vogl, Ueber Milchsaftgefässe in der Klette; Botan. Zeitg., 1866, p. 193.

siderable length, exceeding 3—4 mm; they have a moderately thick membrane which shows no important peculiarity.

The above sacs may occur in certain species of a genus, and be absent in others. Trécul found them in Cirsium arvense, oleraceum, lanceolatum, anglicum, palustre, prælatum: Carduus nutans, crispus, tenuiflorus, Onopordon acanthium: Carlina vulgaris, longifolia, salicifolia: Jurinea alata, Notobasis syriaca, Tyrimnus leucographus, Galactites tomentosa, Duriæi, Silybum marianum, Echenais nutans, Arctium lanuginosum; Lappa communis:—Vernonia eminens, noveboracensis, prælata:—but they are absent, according to the same author, in Vernonia flexuosa Sims., and in the Cynaræ of the genera Cynara, Rhaponticum, Acroptilon, Serratula, Carduncellus, Centaurea.

6. The secretory sacs of the species of **Acer**[1], which are usually called laticiferous vessels from their milky contents, are of cylindrical prismatic form (on the average about 1 mm long and 50–60 μ broad in A. platanoides), and are arranged in rows longitudinally one upon another. Their colourless cellulose walls are as a rule completely closed, the terminal surfaces, which fit one on another, are horizontal or oblique, the lateral surfaces often have short sac-like protrusions, and with these pit-like thinner-walled protrusions they press sometimes between the limiting surfaces of neighbouring parenchymatous cells, sometimes on the lateral walls of other similar sacs. In surface view these thinner-walled protrusions appear as broad, round or transversely elliptical, clearly marked pits, which are smooth, not latticed. I never saw any perforation of the ends. The open lateral communications described by Hanstein, between neighbouring sacs, by means of perforated lateral protrusions, I was also unable to find in sections which had not been macerated: but they were often found just as represented by Hanstein (*l.c.*, Fig. 6) in macerated preparations, even if these (from A. platanoides) had been prepared only by boiling in water. The contents of two sacs, coagulated by boiling into masses, then hung together by a short bridge, which loosely filled a corresponding canal. How far these conditions exist in the living plant, or have arisen as products of maceration, i.e. by rupture of a closed lateral protrusion due to boiling, I must leave undecided.

The sacs are solitary or in groups of 2–4, surrounded by parenchyma: they lie on the limit between the phloem of the vascular bundle and the bundle of sclerenchymatous fibres, which surrounds this externally, at that point in fact where in other plants the first-formed sieve-tubes stand (comp. Chap. VIII): they are also found in the primary bark of branches, and in the petiole and ribs of the leaf. They do not extend further into the parenchyma of the leaf, nor are new ones formed in the secondary bast. Among the species investigated, they are largest and most numerous in A. platanoides. They are developed very early in the internodes, and seem to have special significance during their early stages; still, according to Hartig, they remain filled with sap in the branches of A. platanoides for about ten years. In A. saccharinum and monspessulanum their sap appears, according to Hartig, not to be milky.

7. The peculiar resins of the **Convolvulaceæ**[2] occur in sacs, sometimes as nearly homogeneous masses, but more frequently forming with watery solutions milky mixtures: these sacs have usually been called 'laticiferous vessels' from the latter peculiarity of their contents.

The sacs have been observed in all investigated herbaceous species: they are found, according to the species, in stem, roots, ribs of leaves, or only in certain of these parts: they occur especially in the parenchymatous cortex, and in the bast of the stem and roots: they are ranged one above another in rows, which run longitudinally through the members, and are isolated, or numbers are grouped together: the latter is the case,

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[1] Hartig, Naturgesch. d. forstl. Culturpflanzen, p. 545.—Botan. Zeitg. 1862, p. 98.—Hanstein, *l.c.*

[2] Trécul, Des Laticifères des Convolvulacées; Comptes Rendus, tom. LX. (1865), p. 825.—A. Vogl, Ueber Convolvulus arvensis; Schriften d. Wiener Zool. Bot. Gesellsch. 1863, p. 258.—Idem, Zur Kenntn. d. Milchsaftorgane d. Pfl.; Pringsheim's Jahrb. bd. V. p. 31.

especially in the tuberous roots of Ipomœa Purga, where they form numerous annular zones[1].

Each single sac of a series in slightly elongated members, e.g. in the tuberous roots cited, is short, being not longer, or even shorter than broad: in elongated internodes they attain a considerable length, and an extended cylindrical form with flat or slightly curved ends.

The contents of the sacs are a mass of resin, mixed to a variable extent with watery fluid, and presenting therefore an appearance which varies in different cases (comp. Trécul, *l.c.*); in many investigated cases it contains tannin. The walls are thin, homogeneous, and apparently soft, and show, as far as investigated, no cellulose coloration. With iodine and sulphuric acid they turn yellow: long treatment with the acid does not destroy them.

On the fresh surface of section through the sac-bearing parts the contents of the sacs exude as 'latex,' the more abundantly the longer and more numerous the sacs are. In fresh plants it often appears that the pressure of the contiguous turgescent parenchyma, which presses the milky fluid out from the cut sacs, can burst also the transverse walls, which are not touched in cutting the section, and press out the contents of more deeply-seated members of a series of sacs at the surface of section. I was unable to prove to myself (after investigations on stems and rhizomes of Convolvulus arvensis, Calystegia sepium, dahurica, Pharbitis hispida) either that there is a perforation or solution of the septa within the living plant, and a formation in this manner of long sacs by the coalescence of shorter ones, or that there is a genetic connection, as stated by Vogl, between long sacs and sieve-tubes.

8. The reservoirs of the milky secretion in the Sapotaceæ resemble those of the Convolvulaceæ in many points. Since these are but little known, a report by Herr K. Wilhelm upon an investigation of them conducted by him may be here inserted. He investigated especially Bumelia tenax W., and Sideroxylon mastichodendron Jacq., with which, as far as can be concluded from comparison of dried material, Isonandra Gutta coincides in the main.

The latex of these plants occurs in *completely closed sacs*, which are always surrounded by parenchymatous elements, and differ from these *fundamentally* only in their contents. This is literally true for the *inner cortex*, the reservoirs of latex here found have exactly the form and size of the neighbouring parenchymatous cells. In the *outer cortex* and in the *pith* the laticiferous elements are usually distinguished from the rest by their considerable length and breadth, as well as by their arrangement in uniseriate strings, which run longitudinally through the axis in question, and may be followed to within a short distance of the *punctum vegetationis*. The outer cortex and pith are thus traversed by single rows of laticiferous sacs, which are arranged, at least in the youngest parts of the stem, radially and tangentially perpendicular; new elements are constantly added to these from the apical meristem. As the rows pass downwards in the stem, their originally parallel arrangement is disturbed by the increase of the intermediate parenchyma: they suffer tensions and fractures,—their several parts however remain nevertheless in connection, and at the same time their character as series of distinct sacs is retained. No single case was observed which necessitated or even supported the assumption that, in the living plant, a coalescence of neighbouring members of tubes had taken place as a typical occurrence.

Also in the inner cortex, in the phloem of the vascular ring, it was never possible to prove with certainty a coalescence of parallel laticiferous sacs, or of such as touched at their ends, so as to form extensive reservoirs. In tangential sections the primary arrangement shows no regularity: they usually lie scattered and solitary, but sometimes several occur near to, or one above another, between large parenchymatous cells of similar form. In radial sections they appear sometimes to form long longitudinal

[1] Compare Berg, Atlas, Tab. XXIII.

strings. But careful investigation and comparison of corresponding transverse sections shows that they never appear in the *same* radial planes (or only in rare cases, and then only few of them), but in the large majority of cases in *different* planes.

As the laticiferous sacs of the bast-ring draw nearer to the outer cortex, they lose the milky nature of their contents: they appear constantly more watery, while the sacs themselves become gradually more and more compressed, and finally unrecognisable.

The above relations of distribution and arrangement of the laticiferous reservoirs hold also for the petiole. In the lamina laticiferous sacs appear as elements or concomitants of the nerves, or are found here and there solitary in the parenchyma, in which case they are always characterised there by considerable size.

The *membrane* of the single laticiferous sacs, whether in the outer or inner cortex, the pith, or the leaf, appears in the large majority of cases of equal thickness throughout. It is as a rule *very thin*, and equal to that of the neighbouring cells of the parenchyma, or even thinner. However I recognised in many sacs of the inner cortex partial thickenings of the walls: these appear distributed at many points: they appeared swollen, and a slight protuberance of the outer surface of the cell usually corresponded to such points.—The membranes of the laticiferous sacs are colourless; they give a *blue* reaction with Schultze's solution, but usually the colour is fainter and less pure than that of the surrounding parenchyma.

The *contents* of the laticiferous sacs have sometimes the character of an emulsion, and accordingly appear white by reflected light, showing under the microscope as a finely granular dark mass—this is always the case in the reservoirs of the inner cortex; sometimes they form more or less refractive plugs resembling homogeneous masses of resin: these are usually colourless, or light yellow, and fill the cavity of the sac completely. These plugs can easily be isolated from sections under water, when their behaviour under solvents can be investigated. They occur chiefly in the outer cortex. Carbon disulphide, chloroform, and benzol dissolve the mass almost completely: ether leaves a considerable granular residue. Alcoholic solution of iodine colours it golden yellow. Addition of alcohol removes the resinous appearance, and makes the mass itself dark and finely granular. If freshly isolated pieces of latex be exposed to concentrated sulphuric acid, they are dissolved gradually with a yellow colour: dilute sulphuric acid first produces swelling, while homogeneous drops escape from the substance, the outline of which soon becomes indistinct; their substance then gradually dissolves in the surrounding fluid, and colours it yellow. Meanwhile the original contour of the string of latex is retained: it appears that one substance is extracted while the other remains undissolved. The latter was in many cases found still undissolved after long immersion (two days) in sulphuric acid. Potash produced no apparent change.

In many laticiferous sacs of the outer cortex dusky-looking contents may be found, consisting of numerous drops of the most variable size: they dissolve immediately in water. One is tempted to assume that the before-mentioned resinous contents develop gradually from this latex, which is easily soluble—they occur however in the highest regions of the stem immediately below the *punctum vegetationis*—nevertheless this phenomenon deserves attention, viz. that the resinous plugs in the outer cortex assume, after treatment with alcohol, an appearance which coincides remarkably with that of the contents of the inner cortex. The latter may be completely dissolved by warming with dilute potash: when treated less strongly with this reagent there are sometimes formed from it numerous small crystals or isolated large ones, which disappear quickly on adding acetic acid.

The laticiferous reservoirs of the pith were not accurately investigated as regarded their contents, which coincided exactly in optical properties with that of the sacs in the outer cortex [1].

[1] [On Resin-sacs in Hypericum, compare v. Höhnel, Bot. Ztg. 1882, 149.]

4. *Tannin-Sacs.*

Sect. 35. The secretion of *Tannin* in large quantity in the sacs of Sambucus suggests the idea of placing other sacs or cells with large quantities of tannin in the category of secretory sacs. It is true the presence of this body in large quantity is not decisive, since it occurs also in other places, as in the epidermal cells, and in many plants, especially ligneous ones, particularly in the assimilating, starch-forming parenchyma, and since, as far as we know at present, it is at least undecided whether it appears as a secondary product of the constructive metastasis, as is the case with calcium oxalate, or as an integrating transitional member of it. Further, with the exception of the tannin, too little is known of the structure, and especially of the character of the contents of the organs, which are possibly to be distinguished as tannin-sacs, for us to be able to decide whether, and when, they are to be regarded as secretory sacs, or only as parenchymatous cells rich in tannin. But there are a number of organs which, as far as may be concluded from information at hand, have apparently lost the properties of cells, and are the points of secretion of mixed substances requiring further investigation, amongst which tannin takes *permanently* the most prominent place under the reagents at present in use: these organs correspond further in many cases, in their early appearance and position with regard to the vascular bundles, to the secretory sacs of Sambucus, the Cynareæ, Aceraceæ, &c., also to many intercellular, secretory reservoirs, and may therefore be substitutes for these. Awaiting more exact investigation, and excluding such as contain starch as well as tannin, we may here introduce these organs as *Tannin-sacs.*

They occur as elongated sacs, especially near to the vascular bundles, in the parenchyma of the stem and petiole of many Ferns (Marsilia, Polypodiaceæ, Cyatheaceæ, Marattiaceæ[1], &c.).

Among the families of Monocotyledons, the Araceæ and Musaceæ should be mentioned as having those rows of sacs, to be described in Chap. VI, which accompany the vascular bundles. Also the laticiferous tubes of these plants, consisting of coalesced sacs, would be better placed here than with the rest of the laticiferous tubes in Chap. VI.

Of the Dicotyledons certain Leguminosæ may without doubt be mentioned here. In Phaseolus multiflorus Sachs[2] found in the phloem of the primary vascular bundles of the stem and leaves (but not continued into the root) longitudinal rows of prismatic tannin-sacs arranged singly or in small groups. They form in transverse section a broken series of curves. A similar arrangement appears in a similar place in the transverse section of the branches of Robinia pseudacacia[3]. The sacs are here 6–8 times as long as broad, cylindrical, with rounded ends, and only attached to one another by the flattened middle of the terminal surfaces. A group of rather wider series of sacs, with longer members filled with tannin, lies in these trees in

[1] Von Mohl, Baumfarne, Verm. Schriften, p. 113.—Martius, Icones pl. Crypt. Brasil. Taf. XXXI and XXXIII. Compare also Karsten, Vegetationsorgane d. Palmen, *l. c.* p. 205.—Trécul, Comptes Rendus, Mai, 1871, and Ann. Sci. Nat. 5 sér. tom. XII. p. 373.—Russow, Vergl. Untersuchungen.

[2] Unters. über d. Keimung d. Schminkbohne, Wien (Acad.), 1859.

[3] Hartig, Forstliche Culturpfl. p. 546.

the pith, just opposite each of the vascular bundles: besides these, short sacs are found scattered in the pith.

Many, but not all Leguminosæ are rich in tannin, which is distributed in the tissues in various ways, but in a very constant manner in single species, genera, &c., often without doubt in tissues that do not correspond. The same holds for the Rosifloræ. It remains to be investigated whether also, in many of the cases of the occurrence of tannin enumerated by Trécul, we have to deal with secretory sacs[1].

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[1] Compare Trécul, Du Tannin dans les Légumineuses; Comptes Rendus, tom. LX. p. 225.—Du Tannin dans les Rosacées, Ibid. p. 1035.—See also Sanio, Bem. über den Gerbstoff u. s. Verbreitung, &c.; Botan. Zeitg. 1863, p. 17.—Wigand, Ibid. 1862, p. 121.

CHAPTER IV.

TRACHEÆ.

Sect. 36. Under the above name all those tissue-elements may be grouped which have the following characters: (1) their walls become thickened as they differentiate from the meristem, and lignified to a variable extent, while the thickening is arranged in a fibrous manner, or with bordered pits, or rarely with transverse bars; (2) almost simultaneously the whole protoplasmic body and organised contents of the cells, which are being transformed, disappear altogether, their place being taken by air, or by clear watery fluid. The larger and more elongated tubes falling under this definition were distinguished even by the old anatomists[1], as *Tracheæ*, *Vessels*, Tubes (Vasa, Tracheæ, Fistulæ); more recent investigations[2] have led to the recognition of two subdivisions, which, according to Sanio, may be distinguished as (1) *Tracheides*, and (2) *Vessels* (Vasa) or *Tracheæ*, in the narrower meaning of the word. I shall use the name Tracheæ in this book only as a collective term for both, and specially also in those cases where it is not certainly decided whether a tube belongs to the one or to the other subdivision.

As will be thoroughly discussed in later chapters, the chief points of occurrence of the Tracheæ are the vascular bundles and woody bodies. It may however be at once pointed out here by way of explanation that the above localities are by no means the only ones in which Tracheæ are found. Tracheides are found solitary in the parenchyma (Sect. 55) in many plants, and form the root-sheath characteristic of the aerial roots of Epiphytic orchids[3].

Vessels and Tracheides correspond in the general points of structure: both alike have very various special forms; transitional forms are to be found between them, which will be described more especially in the secondary wood (Chap. XIV). The distinction between them depends entirely upon the mode of connection of the

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[1] Malpighi, Grew, Anat. Plant.—Compare Treviranus, Physiol. I. p. 82; Link, Philosoph. Bot. p. 90, &c.

[2] Sanio, Botan. Zeitg. 1863, p. 113.—Caspary, Monatsbr. d. Berliner Acad. July, 1862.—Caspary terms the organs here called Tracheides, as far as they were the subject of his investigations, 'Leitzellen.'

[3] It need hardly be said that in extending the term Tracheæ to all tissue-elements which correspond in the above peculiarities of structure, without regard to their place of occurrence, it includes also the well-known air- or water-containing, usually fibrous-thickened elements of the leaves of Sphagnum and Leucobryaceæ, they being in fact for the most part Tracheides. Compare on these elements of the mosses, Von Mohl, Verm. Schr. p. 294, and Schimper, Monograph. d. Torfmoose.

elements one with another, and upon certain phenomena of structure of the walls, which will be stated in the description of the latter.

The walls are, as already indicated, always interruptedly thickened, the thickening masses following the well-known rules for cell-membranes[1], and being either pitted, or forming fibrous bands, or both. The form of thickening is either uniform over the whole wall of an element, and even of many contiguous elements, or it varies at different points of one wall-surface, or on different sides of one tube, according to the nature of the neighbouring tissue: these differences are found to be especially frequent in the secondary wood (Chap. XIV). Vessels in which these varieties occur have been called mixed (Vasa mixta)[2].

That part of the wall of the Tracheæ which is slightly or not at all thickened is always a very delicate, almost immeasurably thin film.

According to the form of the thickening mass there are distinguished—

(1) *Tracheæ with fibrous thickening bands*, under which head are ranged—
  (*a*) *Tracheæ with spiral fibrous thickening* (spiral vessels).
  (*b*) *Tracheæ with annular fibrous thickening* (annular vessels).
  (*c*) *Tracheæ with reticulate fibrous thickening* (reticulate vessels).

(2) *Pitted or dotted Tracheæ.*

(3) *Tracheæ with transverse bars* (Tr. trabeculatæ).

The Tracheæ with spiral fibrous thickening (included in I. *a*) were termed true tracheæ (Trachées katexochen) by Mirbel and P. de Candolle (Organogr. I), owing to a false conception of the structure of these and other forms, while the annular and reticulate vessels were called false Tracheæ (fausses trachées) or striped vessels, Vaisseaux rayés, the latter being moreover confused with pitted vessels.

The above forms, especially those with fibrous thickening, often merge into one another, so as to form 'Vasa mixta.' The pitted vessels show in many cases, as will be more thoroughly detailed later, protuberances of the inner surface in the form of fibres usually having a spiral course, more rarely in the form of transverse bars, which traverse the cavity, and give the character to the form (3).

Sect. 37. In the walls with fibrous thickening the strengthening bands extend inwards from the unthickened membrane, usually as relatively narrow flattened ribands, appearing in section of elliptical or rounded-rectangular, or almost quadratic form: in depth (i. e. perpendicular to the surface of the wall) they are less, or not more strongly developed than in breadth (comp. Figs. 56*, 57). They are frequently very flat, broad plates, in the latter case often broken by short, small slits or depressions of the inner surface, e. g. in the spiral or annular tubes of Commelina tuberosa[3]; rarely they are deeper than they are broad, e. g. the closely-wound fibres of the later developed spiral vessels in the stem of Artanthe elongata and other woody Piperaceæ, and especially the annular and spiral bands, like sharp fluting, which protrude far into the cavity in the Tracheæ of the stem of many Cacteæ[4], and

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[1] Hofmeister, Pflanzenzelle, § 25.—Sanio, *l. c.*

[2] Compare P. Moldenhawer, Beitr. p. 185; Von Mohl, Verm. Schr. pp. 278, 279.

[3] Von Mohl, Ueber den Bau der Ringgefässe, Verm. Schriften, p. 285.

[4] Schleiden, Mém. prés. Acad. St. Pétersbourg, sér. VI. tom. IV.—Compare Grundzüge I. (3 Aufl.) p. 259—Trécul, Ann. Sci. Nat. 4 sér. tom. II. pl. 19.

of the leaves of many Mesembryanthema, e. g. M. stramineum. A less common form of the fibres, corresponding to the bordered pits, is that of which the section has the outline of a short-armed recumbent ⊢, while the fibre is attached to the thin wall by the free end of the single (here horizontal) arm. This is the case in the closely-wound spiral tubes, which show transitional forms to the reticulate, and, in many woody stems, are first fully formed when the extension of the internode is ended, as is the case in Artanthe elongata, Nerium, Convolvulus Cneorum. The single arm is

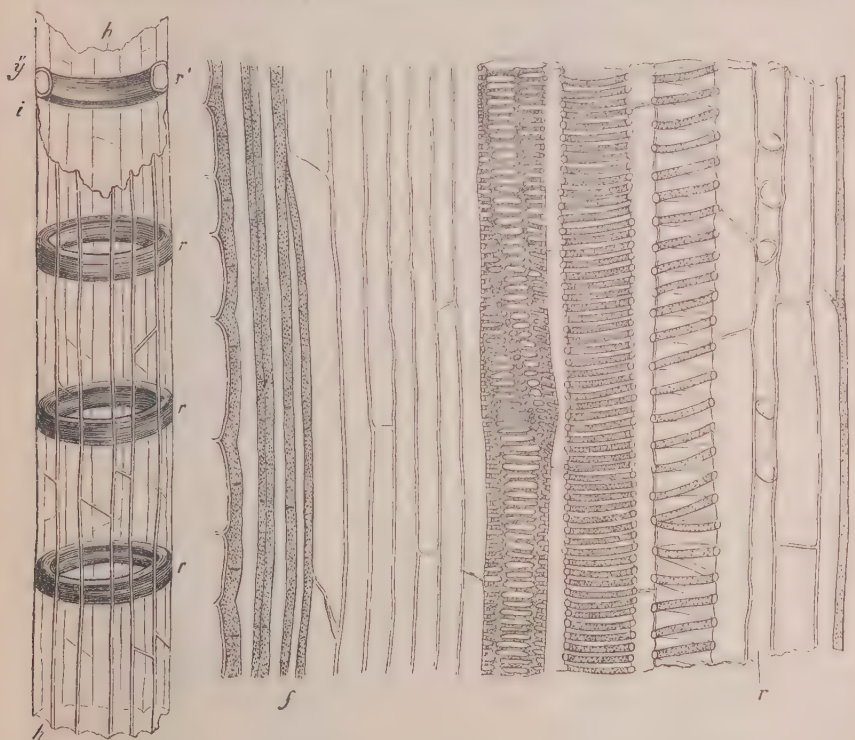

FIG. 56*.—Piece of an annular vessel from the stem of Zea Mais. *h* the thin wall, on which the limits of the adjoining cells are visible, *r* annular fibres, *r'* one of these cut through, *i y* the strata of the same (550). From Sachs' Textbook.

FIG. 57.—Saururus cernuus. Piece of a radial longitudinal section through a vascular bundle of the herbaceous stem; *r* innermost, narrow, distorted annular vessel. To the left of this successively (1) spiral vessel, with loosely wound single fibre, which in two places runs back into itself, so as to form a ring; the thin wall between the spirals of the fibre has given way; (2) spiral vessel with very narrow flattened curve, cut longitudinally in half, with exception of the upper margin; (3) scalariform reticulate vessel; *f* sclerenchyma (or bast) fibres. The curves of the spiral fibres rise in the drawing in the opposite direction to the course they really pursue (375).

in these cases almost always smaller than the two others; in the above-named Artanthe it is very inconspicuous compared with the other strongly-protruding parts.

The *Tracheæ with spiral fibrous thickening* show considerable variety in the number of the fibres, and the steepness and direction of their coils. Their number is often only 1–2 in the narrow tubes, which are first formed when the differentiation of tissues begins, in others 4 or more, and it rises in many cases, e. g. the petiole of Musa, to 16–20. The steepness of the coils is greatest in those tubes which are developed earliest, before the extension of the part to which they belong has ceased: since in these the coils are separated from one another by the

extension which the tube itself undergoes[1]. By this process a spontaneous separation (tearing off?) of the fibre from the elongating wall may occur[2]. If the tube developes later, during or after the close of the extension of the part, the coils are less steep: when several fibres are present they are then arranged at the minimum distance from one another.

The coils rise in most cases (when seen from without) from right to left, that is like the thread of a left-handed screw, or, according to the terminology adopted in Botany, the spiral is right-handed. The opposite direction occurs in Pinus sylvestris (Mohl): in the wood of Vitis vinifera, Berberis vulgaris, Artemisia Abrotanum, Bignonia capreolata, the inmost first-formed tubes are right-handed, the outer later-formed ones left-handed. Where the spiral fibre is interrupted, both the opposite directions of inclination may occur at different heights in one vessel, e. g. the stem of Cucurbita[3].

Not unfrequently, and especially in the closely-wound forms, the spiral fibres are branched, or their coils are connected in a bridge-like manner by oblique or transverse fibrous bands. It is a no less common phenomenon that one fibre at the end of a tube, or at other points, should run back into itself, thus forming a ring. This phenomenon characterises the series of numerous transitional forms between the spiral tubes and the *annular* and *reticulate* tubes, while it gives rise in the latter to a number of special forms of the net. It should be added, in connection with the annular tubes, that the distance of the rings from one another follows the same rules as the steepness of the inclination of the spiral fibres. Besides those above mentioned, there is among the reticulated tubes a varied series of special conformations of the net. Reticulated tubes, the meshes of which are elongated transversely, and arranged on one surface of the wall in a row one above another, being thus comparable to the rungs of a ladder, are called *ladder-like* or *scalariform vessels*, and have frequently been confounded with the pitted vessels, which show a like surface of wall. (Comp. Fig. 56*.)

Individual peculiarities of the tracheides in the sheath of the roots of Orchidaceæ will be brought forward again in Sect. 56.

Sect. 38. It is well known from the general doctrine of cells, that it is only the relative size of the unequally thickened parts of the membrane which gives rise to a general distinction between reticularly thickened and *pitted membranes*, and that therefore there is no sharp limit between these two forms. The wall of the *pitted tracheides* shows sometimes *simple pits*, i. e. not bordered, sometimes *bordered pits*[4].

The term pit is applied to a gap in the internal thickening of the wall, this gap being closed externally by a piece of membrane which is only slightly or not at all thickened. It is in fact a canal varying in length according to the extent of the

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[1] Von Mohl, Veget. Zelle, p. 26.

[2] Compare Sachs, Textbook, 2nd Engl. Ed. p. 90. With this must not be confused that 'unrolling' of spiral fibres, which occurs when a part is torn, and the often-cited 'power of unrolling' of spiral vessels. The latter phenomenon comes about simply by the rupture of the delicate unthickened membrane when the part is torn, while the tough fibre, to which the delicate and easily overlooked tatters of the ruptured wall are attached, is drawn out.

[3] Von Mohl, Verm. Schriften, pp. 287, 321.—Sanio, *l. c.* p. 124.

[4] [Cf. Russow, Zur Kenntniss des Holzes, insonderheit des Coniferenholzes. Orig. communication to Bot. Centralblatt, Nos. 1–5, 1883, in which paper the other principal writings on this subject are referred to.]

thickening, which traverses the wall transversely. If the canal be equally wide throughout or narrowing outwards, we have a non-bordered pit. On the other hand, the term bordered pit is applied to those in which the canal widens suddenly towards the outside, i. e. towards the non-thickened part of the membrane, so that it is here broader than at the part of the canal bordering on the internal cavity. In the surface view of the wall the boundary of the unthickened portion of the membrane

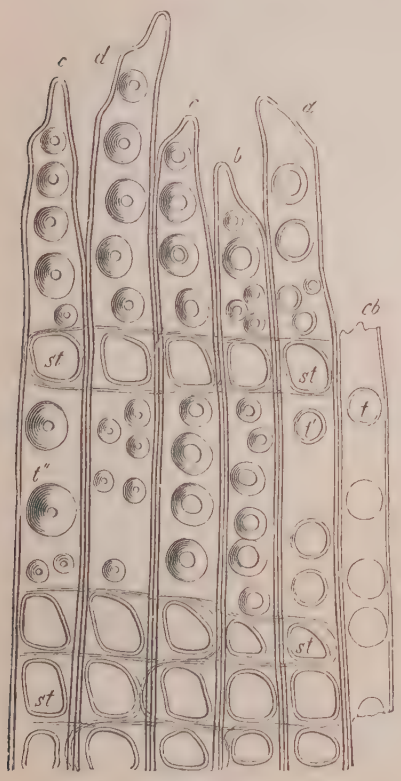

FIG. 58.—Pinus sylvestris; radial longitudinal section through the wood of a branch; *a—e* ends of tracheides with bordered pits (*t'*, *t''* in surface view; *c b* piece of a young wall of a tracheide, with still immature bordered pits; further development of these, successive narrowing of the canal *a—c*; *d* and *e* mature condition; *st* large pits on the limiting surface between tracheides and cells of medullary rays (550). From Sachs' Textbook.

FIG. 59.—Ephedra helvetica. Wood (230); *a* member of a vessel, *b* tracheides seen from the radial side, isolated by maceration with Schultze's mixture; *f* the oblique ends of the member of the vessel in surface view, with two rows of large open bordered pits; at *x*, *x* two closed bordered pits. Of the tracheides, *b* is only drawn in outline, the surface of the other is put in. (The direction of the split-like pits is reversed; they rise in reality from left to right.)

may be seen surrounding the limit of the section of the canal like a border or *halo* (Fig. 58). The widened outer part of the pit, the limit of surface of which is the halo, is called the *cavity of the pit*; in the canal itself may be seen the *outer aperture*, which leads into the cavity of the pit, and the *inner* which borders on

the lumen (comp. Figs. 59–60). The cavity of the pit is in most cases originally and often permanently of the form of a plano-convex lens ('half-lens-shaped'), since the outer surface of the thickening of the membrane, which borders it on one side, is concave, while the unthickened portion of the membrane, which limits it on the other, is flat. The canal is, according to the extent of the thickening of the membrane, either extremely short, so that a sharp-edged opening leads from the lumen of the tube into the cavity of the pit, e. g. in the thin-walled tracheides of the spring wood of Pinus; or, when the thickening is greater, it is elongated, and widens outwards suddenly into the cavity of the pit, e. g. autumn wood of Pinus, pitted vessels of Nerium, Fraxinus, wood-elements of Convolvulus Cneorum, Pteris aquilina (Figs. 61, 64), &c.

The above general description of the structure of the bordered pit is said to hold for those uncommon bordered pits, not belonging to our present subject, which occur in certain *cells* [1], and for those on the limiting surfaces between Tracheæ and other elements; and it is clear that between these and the non-bordered pits only the above-described difference of form exists, which corresponds exactly to that between the flattened and the ⊢ shaped fibrous thickenings. On the surfaces abutting on elements of another order, the bordered pits of the Tracheæ either correspond to non-bordered pits on the walls of these, or they are opposite to an unpitted wall. But where Tracheæ with bordered pits are contiguous with one another, the bordered pits correspond to one another in such a way, that on each limiting surface all the cavities of the pits of the one fit exactly over those of the other. The plano-convex cavities are thus applied to one another in pairs, so as to form the 'lens-shaped pit-cavities' (comp. Figs. 58–62), and each of these is divided by a thin flat lamella of membrane (the limiting lamella) into two halves. This is the case in the first instance in all investigated cases. Also in mature Tracheæ this condition always remains permanent, as can easily be proved in old wood of Pinus, Ephedra (Fig. 60 *b*) [2]. As a rule however the originally plane limiting lamella grows in surface in such a way, that it becomes larger than the median plane of the lens-shaped double cavity, and therefore bulges in a convex manner to one side, and comes into close contact on this side with one of the concave walls of the cavity of the pit (Fig. 60 *c*); meanwhile it remains a very delicate film, but is always, in the cases investigated, thicker in the middle than at its margin. In Pinus sylvestris (and its allies), as first shown by Sanio, the thicker part has the form of a relatively broad plate with a sharply marked

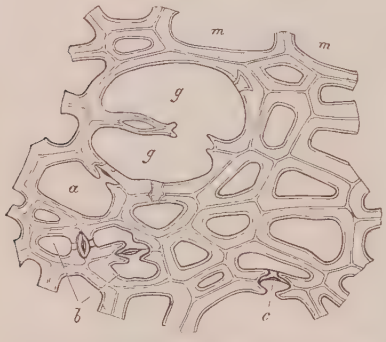

FIG. 60.—Transverse section through the secondary wood of Ephedra helvetica (600); *m* medullary ray, *g*—*g* vessel, the section having passed through the oblique wall separating two members, and in fact through the middle of an open bordered pit (pore), and to the left of this, through the margin of a pit. Besides this vessels and tracheides are transversely cut at *a* and *b*, through the middle of bordered pits of the lateral walls, which have the limiting lamella thickened in a knob-like manner on both sides; at *c* the thickening is on one side.

[1] Compare the figures of the endosperm of Phytelephas (?). Schleiden, Grundzüge, 3 Aufl. p. 232.

[2] Compare Hofmeister, Pflanzenzelle, p. 175.

margin; in Ephedra, which is the most striking instance I know of, it is shaped like a flat biconvex lens; in other relatively small, or at least narrow pits (Cassyta paniculata, vessels of Nerium, Pteris aquilina, &c.), it appears as a hardly perceptible swelling. The thicker portion always lies, like a lid, upon the outer aperture of one of the pit-canals.

The corresponding bordered pits of neighbouring Tracheæ are accordingly closed by the limiting lamella, which occasionally remains plane, but as a rule is applied to one wall of the pit-cavity. On account of its delicacy, and the small size of the whole pit, the limiting lamella, in the form in which it usually occurs, has not hitherto been clearly recognised. In contradiction to Hartig[1] alone, and following the statements of Schacht and Dippel[2], the pit-cavity was regarded as being in the mature state in open communication on both sides with the adjoining cavities of the tubes, while the few cases in which the limiting lamella was observed were considered as exceptions. Sanio[3] has recently clearly proved that in Pinus sylvestris the case is as stated above. I find his statements confirmed in all cases subjected to exact investigation, both in the tracheides of the wood of that tree, and in those of Abies pectinata, excelsa, Juniperus communis; also in the tracheides, and lateral walls of the Tracheæ of Ephedra, and Welwitschia: further in the lateral walls of the 'scalariform vessels' of Ferns (Pteris aquilina); the tracheides of the secondary wood of Dracæna, Cordyline paniculata; the Tracheæ of the wood of Convolvulus Cneorum, Statice monopetala, the large-pitted vessels of the wood of Cassyta (C. paniculata, R. Br.), Nerium Oleander, &c. Extremely good preparations, which are not always easy to obtain, always show the case as described: it should then be characterised at least as the regular condition, and that which is distributed over the most various divisions of the vegetable kingdom. Further investigations must show whether exceptions occur.

While the above fundamental conditions of structure remain constant, the special form of the bordered pit is very variable (compare the Figures 58–62, and what follows in Chaps. VIII and XIV); firstly, according to the length of the canal, which depends upon the extent of thickening of the walls; this has already been mentioned above; secondly, according to the special form of the pit, and of the canal with its outer and inner aperture, as seen most distinctly in surface view of the wall, and according to the relative size of the diameter of these parts in each pit.

All these parts have the forms generally characteristic of pits, which (in surface view of the membrane) vary in individual cases between a circle and a narrow slit. In the same pit all the parts are alike in form, or very similar, as is the case in the circular pits of the tracheides of the wood of Pinus, and the slit-like ones of most scalariform vessels, thus giving rise to the appearance of the bordered pit in surface view as two or three concentric outlines, which differ only in size (e. g. Fig. 58, 61 *B*). On the other hand, the form of the parts may differ in the same pit, either so that they all differ from one another, or one from the rest, and this may occur in all possible combinations. Thus there is a narrow elliptical inner aperture, and a circular outer aperture of the canal, which diminishes greatly towards the outside, with irregularly

[1] Compare especially Botan. Zeitg. 1863, p. 293.

[2] Schacht, De maculis (pits), &c. Programm. Bonn, 1860.—Dippel, Botan. Zeitg. 1860, p. 329.

[3] Pringsheim's Jahrb. Bd. IX. [See also Sachs, in Arbeiten des Bot. Inst. in Würzburg, II. p. 294.]

circular outline of the relatively very large cavity in species of Cassyta: a narrow slit-like inner aperture, and a very small circular outer aperture of the canal, with a broadly elliptical cavity in Elæagnus acuminata: a long and narrow slit-like inner aperture, and a short slit-like outer aperture, with a circular cavity in Aleurites triloba—all these cases occur on the large-pitted vessels of the wood[1].

As regards the relative diameter of the different parts of a pit it is obvious, from what has been premised, that it is always larger for the pit-cavity than for the outer aperture of the canal. The latter is either as large as the inner aperture, or it is smaller than this, and the canal thus becomes narrower outwards to

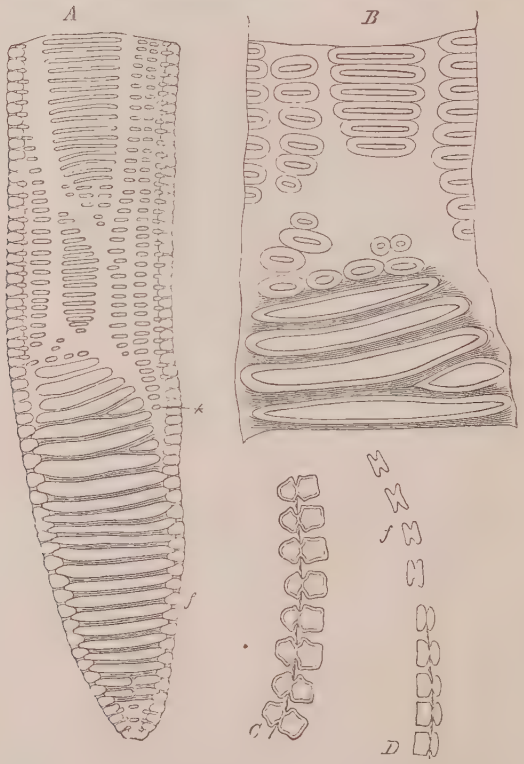

FIG. 61.—Pteris aquilina Rhizome; *A* (142) end, about ⅓ of a short member of a vessel; the oblique ladder-like end surfaces *f*, and a part of the lateral wall in surface view; *B* a piece of *A* at *x*, magnified 375 times; *C* (375) thin longitudinal section through part of a lateral wall, where two vessels touch one another; *D* (375) a similar section through the oblique wall *f* and its margin adjoining the lateral wall. At *f* the pits are open.

a varying extent, and with a form corresponding to the above description: the inner aperture, when of a slit-like form, and differing from the cavity, is always narrower, but often longer than the greatest diameter of the latter. Slit-like bordered pits placed close to one another may thus coalesce internally, in numbers from 2–6, into a common slit, as Mohl found (*l. c.* Figs. 6, 10, 15) in Aleurites and Elæagnus, and

[1] See Von Mohl, Ueber den Bau der getüpfelten Gefässse, Linnæa, 1842; Verm. Schriften, p. 272, Taf. XII.

Sanio (*l. c.* 125) in the wood of Tectona grandis, Fraxinus, Tamarix, &c. This must originate in the thickening of the membrane lasting longer at the inner side than at the outer, and altering its original direction at a later period. On the vessels of the wood of Mahonia aquifolium Sanio found round bordered pits, arranged in left-handed oblique series, with the inner apertures serially coalescent into long slits, while between these the thickening of the walls protruded inwards in form of spiral bands.

The arrangement of the bordered pits on a wall-surface differs in no way from the known rules for the arrangement of pits generally. They are arranged on a surface in perpendicular, horizontal, or, especially when of slit-like form, in oblique spiral series: in the latter case the spirals are almost always left-handed: the number of these series varies according to the special cases, and on equal areas it varies on the whole inversely with the size of the pits. We may cite as examples of extreme cases, on the one hand, the usually loose series of large round-bordered pits on each radial face of the tracheides in the wood of Pinus, and the several loose series of large pits on the wide vessels of the wood of Cassyta (Mohl, *l. c.* Fig. 1); on the other hand the walls covered with close and small pits, which are found surrounding the large vessels in the vascular bundles of the stem of the Cucumber, the tubers of Dahlia[1], many Dicotyledonous woods, as Quercus, Nerium, &c., &c.: in these cases the margins of the pit-cavities are separated from one another by quite narrow bands or ridges of the wall.

A special case of frequent occurrence may here be mentioned, viz. the transverse, slit-like bordered pits, which are characteristic of almost all Ferns (Fig. 61), and which also appear in many Dicotyledonous woods, as Cheilanthus arboreus, Vitis[2], &c., these being arranged like the rungs of a ladder, in one or few longitudinal perpendicular rows on a single wall-surface. The wall-surfaces on which they occur may be called scalariform or ladder-like surfaces, while these Tracheæ, together with the similar reticulate tubes above mentioned[3], have been termed scalariform or ladder-like vessels, Vasa scalariformia, also scalariform tubes. It is useful to distinguish them from the reticulate vessels with non-bordered, transverse pits, either as bordered scalariform surfaces or Tracheæ, or to reserve specially for them the name of ladder-like or scalariform surfaces.

Sect. 39. As one of the above-described forms of wall-thickening there are found, in some few cases to be cited below, ingrowths of the thickened portions of the membrane, which protrude in a conical or bar-like form into the cell-cavity, or are stretched transversely across it: and those Tracheæ in which these are largely developed may be distinguished by the name, introduced above as No. 3 (p. 156), viz. *Tracheæ with transverse bars*. The bars are very largely developed in the narrow primary tracheides occupying the corners of the vascular bundles of the stems of the stronger species of Lycopodium, and in the margin of the vascular bundles of the leaves of Juniperus[4] (comp. Chap. VIII). They are here somewhat flattened cylindrical fibres, branching irregularly on all sides, and with the branches connected on the one hand one with another to form a net spread through the cavity, and

[1] Compare Sachs, Textbook, 2nd English Ed., p. 26. [2] Von Mohl, *l. c.*

[3] Compare Link, Elem. Phil. Botan. Ed. 1, p. 95; Von Mohl, Veget. Zelle, p. 27; Unger, Anatomie und Physiologie, p. 172. [4] Compare Von Mohl, Botan. Zeitg. 1871, p. 12.

attached on the other to the thickened lateral wall of the tracheide. In the tracheides of the leaves of Juniperus (Fig. 62), their points of attachment and origin are especially the thick swollen margins of the bordered pits, in the Lycopodia the spiral or reticulate bands with which the lateral wall is thickened. At the corners of the vascular bundles of the leaves of Biota orientalis the swollen margin of the bordered pits is often elongated into blunt cones, which protrude into the cavity, but here end blind, without branching or coalescing with one another or with the opposite wall. As a rare and anomalous phenomenon Sanio[1] found single simple bars, stretched transversely from one wall-surface to the opposite one, in single tracheides of the wood of Hippophae rhamnoides, and Pinus sylvestris: in the latter they are stretched between the tangential walls, and where they occur at all they traverse in the same direction the entire length of long radial series of tracheides, as far as the cambial zone. (Comp. Chap. XIV.)

FIG. 62.—Juniperus communis; leaf, transverse section (600), *p* parenchymatous cell; next to it tracheides of the corner of the vascular bundle, with bordered pits, and reticulately-branched transverse bars. The parts lying below the surface of section focussed are shaded.

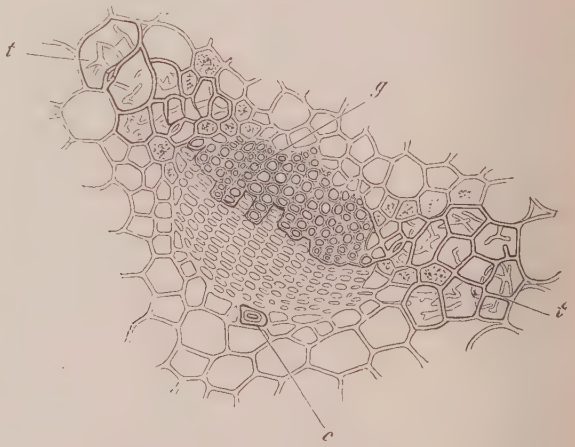

FIG. 63.—The same (225); vascular bundle, *g* xylem, *c* single sclerenchymatous fibre at the outer limit of the phloem; *t* margin consisting of tracheides with bordered pits and transverse bars. The parenchymatous cells near and between the latter are shaded with dots.

Further details on the structure of the walls of the Tracheæ will be described in later chapters, especially the VIIIth and XIVth.

SECT. 40. The wall of the Tracheæ, whatever be its structure, is in the one series of cases a completely closed membrane (*Tracheides*); or it is broken through at the limiting surfaces between elements placed serially one above another, and originally completely closed, the series thus coalescing to a continuous tube, which is called a *vessel*. The tracheides therefore differ from the vessels only in the absence of the holes which occur in certain of the walls, and thus connect the cell-cavities. Transitions between them occur in the secondary wood of Dicotyledonous plants (comp. Chap. XIV), e. g. Leguminosæ, inasmuch as with otherwise similar characters the holes are absent in one case and present in another. Holes are also to be found in

[1] Botan. Zeitg. 1863, p. 117.—Pringsheim's Jahrb. Bd. IX. p. 59.

the elements of the root-sheath of many Orchids (Sect. 56), but these had better be termed generally tracheides, since the connection in rows which is characteristic of vessels is absent.

The *Tracheides* are in some few definite cases—ends of vascular bundles, transfusion tissue, the root-sheath of Orchids—short, even iso-diametric sacs: as a rule they are of the form of elongated, spindle-shaped, fibrous cells, pointed at the ends, and with round or polygonal transverse section. They usually remain microscopically small, their length, which is a large multiple of their breadth, reaches 0·16^{mm} to about 1·00^{mm}: this is the case in the wood of most Dicotyledons[1]: or it rises to 4^{mm}, as in the later annual rings of Pinus[2]: in many cases however they attain great dimensions: the large spindle-shaped spiral and annular tubes in the stem and petiole of Musa and Canna[3] attain a width of 0·08 to 0·10^{mm}, and are always more than 1^{cm} in length; the spiral tubes of Nelumbium speciosum have, according to Caspary, a length of over 12^{cm}, and width of 0·567^{mm}. The great majority of Tracheæ belong to the category of tracheides: for instance, the tracheal elements of all peripheral ends and expansions of vascular bundles, of the secondary wood of the Coniferæ, Cycadeæ, most elements of the secondary wood of woody Dicotyledons, almost all Tracheæ of the Ferns, in the widest sense—vessels are only known to occur in Pteris aquilina, and in the root of Athyrium filix femina[4]—the Tracheæ of the vascular bundles in stem and leaf of the Cycadeæ and Coniferæ[5], of many, though far from all Monocotyledons, and numerous Dicotyledons[6]. Many even of the most striking elements with fibrous thickening, usually described as vessels, belong to this series. To the already-cited examples of Canna, Musa, and Nelumbium we may, according to Caspary's work quoted above, and referring to this for further details, add the following examples: the 'vessels' in the vascular bundles of Stratiotes aloides (stem), Caladium nymphæifolium, Pistia Stratiotes, Acropera Loddigesii, Aerides odorata, Alisma Plantago, Sagittaria sagittæfolia, Hydrocleis Humboldtii, Musa spec. (vessels in this case in the root), Brasenia peltata, Nuphar luteum, pumilum, Nymphæa alba, gigantea, Victoria regia, Monotropa Hypopitys. A general view of the occurrence of tracheides and of true Tracheæ will only be possible when the necessary arduous investigations have been extended over a larger number of cases than has hitherto been the case.

Sect. 41. A **vessel** arises from a series of originally-separate cells, placed one above another, by the perforation, at the close of the process of thickening, of the division walls between the members of the series, the latter being then termed the *members* of the vessel.

The rows of cells, above indicated (pp. 9 and 11, in Figs. 2 and 4) by the letter *v*, which extend to the apex of the plerome, and similar ones marked *g* in Fig. 3, p. 10, are rudiments of vessels.

The members are also always easily distinguishable in a mature vessel, and are

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[1] Sanio, Botan. Zeitg. 1863, p. 114. [2] Sanio, in Pringsheim's Jahrb. VIII. p. 401, &c.

[3] Compare Unger, Anat. und Physiol. p. 171, and p. 218, Fig. 92 *b*.

[4] Russow, Vergl. Untersuchungen, p. 103.

[5] Mettenius, Beitr. zur Anat. d. Cycadeen, p. 258. [See also V. Höhnel, Ueber das Vorkommen von Gefässartig-zusammenhängenden Tracheiden-strängen in Coniferen-hölzern, Bot. Ztg. 1879, p. 329.]

[6] Caspary, Monatsbr. d. Berl. Acad., Juli, 1862.

separable from one another, their limits being marked by their margins, which are always permanent, often also by other portions of the perforated dividing wall: these portions have the structure of a thickened double cell-membrane, and consist of two thickening plates and a simple limiting lamella between them. Schultze's mixture, or hot solution of potash, destroys the limiting lamella, and thus separates the members from one another.

The form of a member of a vessel is as a rule cylindrical or prismatic, the breadth being throughout almost uniform, or diminishing quite gradually towards one end: more rarely each member widens in the middle to a barrel-shape. The length of a member is usually greater than the diameter: it is very much greater in the vessels with a loose spiral, or in annular vessels, which develop before the extension of a part is complete, and thus grow greatly in length as the part elongates. The members of such vessels as arise after the extension of a portion of a stem or root is complete are composed of short members, these being barely longer or even shorter than they are broad, e. g. the wide-pitted and reticulate vessels of old stems of Cucurbita, Cobæa, Vitis, &c. (comp. Chap. XIV). Successive members of a vessel are as a rule of almost similar form through long tracts, though they often decrease gradually in width. The general form of the vessel may be concluded from these data: such as are composed of short barrel-shaped members were distinguished by the old authors as rosary-shaped: Vasa moniliformia.

The walls, by which the members of the vessel are in contact with one another, are either horizontal, in which case those of the successive members fit exactly on one another, and together form the septum (comp. e. g. Fig. 3, *g*), or they are more or less oblique, and the inclined faces of successive members here also fit exactly throughout so as to form the oblique septum (Figs. 59–61): or the ends are oblique and pointed, and only a part of the opposed faces of successive members is united so as to form a septum, near and above which the pointed end forms a blind and often irregularly-formed continuation.

The perforation of the septum is always brought about thus: on the delicate primary membrane one or several flat large pits are formed by the typical process of thickening; the unthickened parts of the membrane are then at once dissolved and disappear, while the thickened bands of membrane, connected directly with the thickenings of the lateral walls, remain persistent. In almost all cases on horizontal septa, and not uncommonly on oblique ones, there appears one single pit, or one single round or elliptical opening, which then always occupies the greater part of the surface of the septum, and often, especially in thin-walled vessels, the whole surface with exception of a very narrow peripheral band. On the other hand, strongly-inclined septa, and very rarely horizontal ones (Avicennia), retain in most cases several or many openings included within the thickened margin, and separated from one another by thickened bands. These are in some few cases round, e. g. in the Tracheæ of Ephedra[1] (Fig. 59), usually they have the form of slits of varying breadth, and arranged parallel in rows, whence the expression *ladder-like perforated* septa (Fig. 61). The slits are usually almost at right angles to the longitudinal axis of the vessel, and the series of them are similarly

[1] Von Mohl, Ueber den Bau d. grossen getüpfelten Gefässe von Ephedra; Verm. Schr. p. 268.

arranged: thus the narrow, closely-grouped transverse slits in the ladder-like oblique walls of the pitted vessels in the wood of the Betulaceæ, Ericaceæ, of Corylus, Carpinus, Pteris aquilina; the round openings of the oblique walls of Ephedra arranged in 1–2–3 rows, &c. Rarely the slits are parallel to the longitudinal axis of the vessel: e. g. vessels of Hieracium vulgatum, Onopordon Acanthium, in which irregular reticulate openings also occur. In an Avicennia Sanio found the horizontal septum surrounded by a sharply-marked thickened margin, and the whole remaining surface covered with many irregular, round or slit-shaped, bordered openings[1]. There is no constant relation between the form of thickening of the lateral wall and the form of perforation. Nevertheless most vessels with fibrous-thickening have round openings, and very many vessels with bordered pits have ladder-like perforations. In pitted vessels, however, simple openings are also frequent, and Sanio found ladder-like perforations in the spiral vessels of species of Casuarina, Olea europæa, and Vitis.

In thin-walled vessels—such as most of those with fibrous thickening, and thin-walled pitted vessels, e. g. in the wood of Betulaceæ and of Tilia—the margin of the opening of the septum is smooth and thin, corresponding to the margin of very flat, not bordered pits. In thick-walled vessels it is thicker, and has the structure of a pair of corresponding bordered pits opened by disappearance of the limiting lamella, and with but small difference of width between the pit-cavity and the wide orifice of the pit: it consists therefore of two acutely-diverging lamellæ. In many vessels this structure as of a bordered pit is extremely striking, e. g. in the large solitary openings of the pitted vessels in the wood of Nerium, Fraxinus, Convolvulus Cneorum (Fig. 64), Pirus torminalis[2], in the serially-arranged round openings of the vessels of Ephedra (Fig. 60, *g*), and the small slits of the scalariform vessels of Pteris aquilina (Fig. 61). It also occurs very plainly in the thick and closely-wound spiral vessels in the stem of Nerium. In other cases, even when the margin of the opening is very thick, it is often only slightly indicated by a small indentation running over the limiting lamella of the margin: e. g. the pitted vessels of Cucurbita, Juglans, Acer monspessulanum (Dippel, *l. c.*). The history of development shows, in the cases of the latter category, that the opening arises by the

FIG. 64.—Convolvulus Cneorum, wood, transverse section (600); *g*, *g* small vessels cut transversely through the oblique septum. The rest are tracheides. At *t* the very delicate closing membrane of the bordered pit is visible.

[1] Sanio, Botan. Zeitg. 1863, p. 121.—Von Mohl, *l. c.*

[2] Compare Dippel, Botan. Zeitg. 1860, p. 329.

disappearance of the limiting lamella in the face of a young pair of wide corresponding bordered pits.

Since the structure of the bordered edges of the apertures corresponds to that of closed bordered pits, the practical decision whether in a given case an open or a closed pit is present is necessarily extremely difficult, if the parts of the septum in question be small, and resemble closely the bordered pits of the lateral walls in form and size; and the difficulty is the greater, since in such cases intermediate forms between the open and closed bordered pits—which are never exactly alike—occur at the limits between the septum and the lateral walls. The apertures at the middle of the septum in the pitted vessels of Ephedra (e.g. Fig. 59, *f*) are larger than the closed bordered pits of the lateral walls. But at the margin of the septum there occur not unfrequently round bordered pits (Fig. 59, *x*), which, though resembling the apertures in form and size, are closed like the pits of the lateral wall. In the large scalariform vessels in the rhizome of Pteris aquilina (comp. Fig. 61) the transverse, bordered, slit-like pits of the lateral walls are always closed. The strongly-inclined septa or terminal faces of the obliquely pointed members of the vessels show a quite similar ladder-like series of slit-shaped pits, like those of the lateral walls, but with the difference that here the slit-like pits are wider, and the thickened intervening bands which separate them are thinner than on the lateral walls. In the middle of the septum the slits are open, as is plainly shown in sections through vascular bundles which have been injected with glue and then dried, if the sections be then treated with water and the glue dissolved. The bands between the slits then separate from one another (Fig. 61, *D*, *f*). Towards the ends of the intervening wall the pits are, on the other hand, of the same width as the open ones, but closed by a limiting lamella: on the corners of the lateral walls they become gradually narrower, and like those of the lateral walls.

The vessels are not unfrequently branched, two or more series of members being attached laterally to one member. When such branches run parallel or converge, they may attach themselves again laterally to a single series of members; a vessel may thus be in its longitudinal course alternately single and double[1].

As regards the *absolute size* of the vessels, there is nothing to oppose the view that their *length* may equal that of the whole plant, or at least may be very great. At all events, on following the vascular bundles through long distances, member is found attached to member, while blind-ends are rare, except in the ends of the peripheral expansions of the plant. The width of the vessels is extremely unequal, and changes variously according to the point of their occurrence in a given plant, and according to the single species or genus. It may be said generally that the diameter does not on the average exceed that of narrow fibrous cells in those vessels which appear first in stems and roots, before the extension is complete (spiral and annular), and in those which traverse the nervation of the leaf. Those formed in stems and roots at the end of the process of extension, or subsequently, may in many cases attain much greater width, while this does not prevent others of the smallest calibre occurring with or near the former. For examples of this see Chap. XIV. Vessels of greatest width occur in the central part of the vascular bundles of many

[1] Von Mohl, Palm. Structura; Verm. Schriften, p. 142.

Palm stems[1] (compare Chap. VIII), where they attain a diameter of 0·280mm (Mauritia armata) to 0·562mm (Calamus Draco); in the wood of many climbing and twining plants, e. g. Cucurbita, Cobæa, Phytocrene[2], Ampelideæ, in which also the width may rise to 0·3 — 0·5mm, &c.[3] The vessels of greatest width are always pitted vessels with short members.

After what has above been said on longitudinal course and branching, it need hardly be noticed further that in one and the same vessel the width (and with it the form of thickening of the walls) may often change in successive parts of its course, i. e. in its successive members; for instance, Mohl states the diameter of the above vessels of the Palm-stems at the lower ends of the bundles as 0·011 mm.

As regards the material composing the walls of Tracheæ and Tracheides, it is certain that they are, when first formed, cellulose membranes, and that they consist, when mature, of more or less lignified cellulose. The lignification is present to a very varying extent according to the special case; in hard, firm parts more than in soft, sappy parts; the Tracheæ of delicate foliage-leaves, or of sappy stems, &c., often show an almost pure cellulose reaction. A very remarkable phenomenon, to which Burgerstein has recently again drawn attention, is the surprisingly early appearance of lignification in many vessels. It is beyond the scope of this work to enter minutely into the process of lignification: it cannot at present be exactly stated how far it shows peculiarities in the several organs in question. Reference may therefore only be made here to works upon the subject: the summary of the older results in Hofmeister, Pflanzenzelle, Sect. 30, Kabsch, Pringsheim's Jahrb. III, and the newest investigation of A. Burgerstein, Sitzungsber. d. Wiener. Acad. Bd. 70, July, 1874.

Sect. 42. All Tracheæ are alike in the peculiarity that when they are fully formed the protoplasmic body disappears entirely, without leaving any vestiges behind, as is the case in dried-up cells. The membrane alone remains of the components of the cell. The space surrounded by it is filled in the mature tube with very dilute watery fluids, which may here be called shortly water, or with air, or with both together. The large majority of Tracheæ are entirely or for the most part filled with air at the time of full development. The extremely thin layer of fluid on the inner surface, which is always difficult to observe, is often beyond anatomical demonstration: even in cases of excessive supply of water in bleeding parts air bubbles occur in the fluid contained in them[4]. It is only in lateral extensions of the vascular bundles of certain plants (Transfusion tissue, Chap. VIII) and in the endings of bundles that they are exclusively filled with water. The same holds for the rudimentary Tracheæ of many water plants.

A remarkable exception to this occurs very generally in plants which contain latex, or resinous, or tannin-containing secretions, whether the latter be stored in the sacs treated of in Sections 33 and 34, or in intercellular reservoirs (Chap. VII). A greater or less number of *vessels* are often filled in these plants for a greater or less distance with latex, or with some such characteristic secretion. No fixed rule is to be found as to the position of these vessels relatively to the other normal air-containing vessels, or to the secretory reservoirs. How the secretion gets into the vessels is not

[1] Compare Von Mohl, Bau des Palmenstammes; Verm. Schr. p. 142.

[2] Mettenius, Beitr. zur Botanik, p. 50.

[3] [Compare Westermaier u. Ambronn, Lebensweise u. Structur d. Schling- u. Kletter-pflanzen, Flora, 1880.]

[4] Compare Hofmeister, Flora, 1850, p. 2.

explained in plants without laticiferous tubes, though plausible conjectures may be made on the subject. The same holds as a matter of fact also for plants with laticiferous tubes, but there are controversies on this point, which we shall return to in Chap. VI.

The frequent filling up of the cavity in the Tracheæ, e. g. in old layers of wood of Coniferæ and many Dicotyledons, with resin or resin-like masses is undoubtedly a phenomenon of incipient degradation and disorganisation. It will be further treated of in Chap. XIV.

In old or damaged, large, tubular Tracheæ the internal cavity is not unfrequently partially or completely filled with parenchymatous cells (Füllzellen), which in the wood of the chestnut drew the attention of Malpighi[1]: they have since been frequently described, and have been termed by the anonymous writer in the Botanische Zeitung[2] *Thyloses* (Thyllen).

They may arise where a Trachea borders on parenchymatous cells, and in fact from those cells themselves, which grow into it. A small part of the membrane of a parenchymatous cell adjoining an unthickened point on the wall of a Trachea (as a rule a pit) grows to an excrescence protruding into the cavity of the latter: it contains protoplasm, usually with a well-marked nucleus, and expands from a blunt and short cylindrical form to a round, often voluminous bladder, and finally cuts itself off as a special cell from the rest of the cavity of the cell which produced it by means of a division-wall, formed at its point of entrance into the Trachea. Thus there always arise at first solitary bladder-like cells protruding from the wall into the cavity of the tube. The process may be arrested at this point: but often the phenomenon is extended quickly over numerous points of a portion of a tube, so that the latter gradually becomes entirely coated internally with the cells, and these, as they extend, gradually fill it up completely. This often happens to such an extent that the tube is entirely filled by thyloses flattened into polyhedral forms by reciprocal pressure. Further, a multiplication of them by division has been observed in many cases[3].

The parenchymatous cells bordering on a tube take part unequally without recognisable rule in the formation of thyloses: some throw out thyloses at one point, others at several, others again not at all. The formation of fresh thyloses may continue for a long time in a portion of a vessel: in vessels several years old (e. g. in an eight years' old layer of wood of Vitis, Reess, *l. c.*) the first beginnings of new thyloses often occur in close proximity to others apparently several years old.

The cellulose wall of the thyloses, which is at first delicate, is later thickened in woody plants, and often has corresponding pits on the surfaces of contact with other thyloses. In the same plants starch may be stored up in their contents, as is the case in normal parenchymatous cells.

The formation of thyloses has been observed in Monocotyledons (Arundo

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[1] Anat. Plant. p. 9, Tab. VI. fig. 23.

[2] Vol. for 1845, p. 225. Θύλακος = sac, bag, reservoir. In this treatise the older literature on the subject is referred to. For more recent information see Reess, Zur Kritik der Böhm'schen Ansicht über die Thyllen, Botan. Zeitg. 1868, p. 1; Unger, Ueber d. Ausfullung alternder u. verletzter Spiralgefässe durch Zellgewebe, Sitzungsber. d. Wiener Acad. Bd. 56 (1867).

[3] Trécul, Sur l'origine des bourgeons adventifs; Ann. Sci. Nat. 3 sér. tom. VIII (Maclura).—A. Gris, Ann. Sci. Nat. 5 sér. tom. XIV. p. 38 (Cissus).

Donax, Canna, Hedychium, Strelitzia, Musa, Palms), and in the wood of very many Dicotyledons, both in one-year-old stems (Canna, Cucurbita, Bryonia, Cucumis, Solanum tuberosum), Euphorbia helioscopia, &c., and especially in long-lived stems of Dicotyledonous woody plants, where they are very widely distributed, and easily observed phenomena, e. g. in Vitis, Quercus, Sambucus, Platanus, Robinia, &c. But in the roots of Dicotyledonous trees, which have been examined for them (Quercus, Fraxinus, Fagus, Betula, &c.), they do not occur, or extremely rarely [1]: in the roots of herbaceous plants, however, they occur in large quantity: Pharbitis hispida, young strong roots of Cucurbita, Urtica, Rubia, &c.

The tubes in which thyloses appear are in most cases typical, wide-pitted vessels: but in Canna (and also in Musa and its allies) they are also the above-mentioned (p. 165) wide, fibrously-thickened non-perforated, tracheides.

In the pitted vessels of many Dicotyledonous woody plants the formation of thyloses is a regular phenomenon, which appears in the normal uninjured plant, though not extending to all pitted vessels. In Robinia pseudacacia it is stated that the pitted vessels of the wood (and, according to Gris, all the vessels) begin to be filled with thyloses in the autumn of the year in the spring of which they were formed, and that these are at times filled with starch. Other woods behave in the same way as regards the time of first formation of thyloses, but no definite rule has been recognised for their occurrence or absence; e. g. in Vitis, Quercus robur, Platanus, according to Reess. Injuries by which the vessels are opened are, as far as investigated, without influence on the formation of thyloses in woody plants. In the large tracheides of the stem of Canna, however, they occur, according to Unger, if these have been injured, e. g. cut into, and then exposed to air or water. These facts may afford starting-points for the inquiry into the still unknown causes of the formation of thyloses, which cannot be further noticed here.

[1] Von Mohl, Botan. Zeitg. 1859, p. 294, and earlier.

CHAPTER V.

SIEVE-TUBES.

Sect. 43. The Sieve-tubes, Tubi cribrosi, were first clearly distinguished by Th. Hartig[1], in the year 1837, as essential constituents of the bast and of the vascular bundles of Phanerogams, and were in some cases designated by the above name, while in others they were termed sieve-fibres. After lying unrecognised for many years, Hartig's observations were confirmed and extended, especially by Mohl, Nägeli, and Hanstein[2].

The chief points of occurrence of the organs in question are those above mentioned; they are rarely found elsewhere. They are present in both Phanerogams and Ferns. They have been most thoroughly investigated in the *Angiosperms*. They may therefore be treated of first as they occur in the latter plants, and afterwards the peculiarities to be found in the other divisions may be added.

The articulation of the sieve-tubes in the plants in question is throughout similar to that of the vessels treated in the preceding chapter. They arise from longitudinal rows of elongated, cylindrical, or prismatic cells, and these remain always clearly distinguishable and separable as their *members*. On the faces with which the members are mutually contiguous they come into open communication through the *sieve-plates* or *sieve-fields*, which are circumscribed portions of the wall, by means of numerous very small, perforated pits, the *pores* of the sieve.

The form of the members of the tubes is that above stated. Their ends are limited by *one* flat, or slightly concave wall (concave on the under side); and this is either almost horizontal, or at most slightly oblique, and in that case as a rule slightly broader than the middle of the member; or it is very strongly inclined, and cuts the lateral-wall on one side at a very acute angle, so that each end of a member is bevelled on one side like a chisel. The inclination of the terminal surfaces is in the latter case—though not invariably and exactly—towards the radial plane.

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[1] Vergl. Untersuchungen über die Organisation des Stammes d. einheim. Waldbaüme; in Jahresber. üb. d. Fortschritte d. Forstwissenschaft, &c. p. 125.—Compare further Hartig, Vollst. Naturgesch. d. forstl. Culturpfl. Berlin, 1851; Botan. Zeitg. 1853, p. 571.—Ibid. 1854, p. 51.

[2] Von Mohl, Einige Andeutungen über d. Bau d. Bastes, Botan. Zeitg. 1855, p. 865.—Nägeli, Ueber d. Siebröhren, Sitzsber. d. Münchener Acad. Feb. 1861.—Hanstein, Die Milchsaftgefässe u. verw. Organe, &c. Berl. 1864.—Mohl calls the members of sieve-tubes '*latticed cells*' (Gitterzellen). P. Moldenhawer had already distinguished them in part as '*vasa propria*,' but confused them with other elements under this name. [See further Wilhelm, Beiträge z. Kenntniss d. Siebröhren-apparates Dicotyler Pflanzen, Leipzig, 1880.—Janczewski, Sur les tubes cribreux, Mém. Soc. Cherbourg. 1881. —Idem, Ét. Comp. sur les tubes cribreux, Ann. Sci. Nat. 6 sér. tom. XIV. 1882.—Russow, Sur la structure et le développement des tubes cribreux, Ann. Sci. Nat. 6 sér. tom. XIV. 1882.]

The first of these two chief forms, which may be termed that with transverse or flat ends, is by far the most general, and is almost exclusively present in the 'primary' vascular bundles (Chap. VIII); the second, or sharp-ended form, preponderates equally in the secondary bast of Dicotyledons. Exceptions are however found to this rule, e.g. the beautifully-bevelled members of tubes in the vascular bundles of stems of Calamus, and the roots of Aroideæ (e. g. Philodendron Imbe); and on the other hand the flat-ended tubes of the secondary bast of Fagus sylvatica, Quillaja saponaria, Ficus elastica, Maclura, &c.

The size of the members of the sieve-tubes varies, especially in different species, no less than that of the vessels. The same rules hold for the length of their members as for those of the vessels: but the maxima of diameter of the latter are not attained by the widest sieve-tubes. The widest sieve-tubes attain a diameter on the average not more than 0.02 mm to 0.08 mm: Cucurbita; species of Bignonia, Phytocrene, Calamus, &c. On the other hand, extremely narrow and insignificant ones are to be found, especially in many, but not all, succulent plants, and in such as have latex (e. g. Asclepiadaceæ, Crassulaceæ, &c. Comp. Chap. VIII).

A few measurements of large members of sieve-tubes may be given below, but with the remark that the measurements of length in long members are only approximately made, or from single specimens, owing to the extreme difficulty of neatly isolating such delicate organs.

Internodes of	Length. *mm.*	Diameter. *mm.*
Cucurbita Pepo	0·370—0·450	0·045—0·050
Lagenaria vulgaris	0·125—0·200	0·025—0·040
Calamus Rotang	over 2 mm	0·030—0·050
Potamogeton natans	0·275	to 0·025
Bignonia spec. (Mohl)	to 1·35	0·450
Vitis vinifera, bast	about 0·6	
Root of Philodendron Imbe	to more than 2 mm.	

As regards the longitudinal and lateral connections of the members, and the branchings which in certain cases are thus produced, the same rules apply in the main as in the case of the vessels.

The walls of the sieve-tubes are always delicate, not lignified, colourless cellulose membranes. The sieve-plates characteristic of them only occur on those surfaces where the members abut on similar elements. The sieve-plate is a sharply-limited part of the wall, like a large shallow pit, which is originally, and often throughout life, less thickened over its whole surface than the wall surrounding it. It is thickly covered over its whole extent with round or polygonal secondary pits, which are separated from one another by narrow bands of membrane: it thus resembles a fine sieve, net, or lattice (Figs. 65–73). The sieve-plates of members of tubes which are contiguous fit with all their secondary pits exactly on one another, and in them the intervening wall disappears when the differentiation of tissues begins, so that holes—the *sieve-pores*—appear, through which an open communication is established between the neighbouring members.

The original width of the sieve-pores differs according to the special case. The widest occur in the Cucurbitaceæ, where the largest (Cucurbita, Lagenaria) attain a size of 5 μ and more: most of them are much narrower; in the above-named Cucurbitaceæ only 2 μ wide; also for the bast of Bignonia spec. Mohl states it at 2 μ,

which would be too high an average for most plants: in many Angiosperms with small sieve-tubes they are certainly narrower, often being on the limit of clear recognition.

Further in the same plant, and even in plates lying close together, the width of the pores is very unequal: in the large tubes of Cucurbita and Lagenaria, where exact measurement is possible, the diameter of the pores of neighbouring, and otherwise equally developed plates may differ by three times (comp. Fig. 65). In one and the same plate the difference in size of the pores is usually small, if at all recognisable: according to Nägeli they are, at least in Cucurbita, wider on the average at the middle than at the margin of the plate. Very considerable differences in size and form on the same plate are rare. (Comp. Hanstein, *l. c.*, Taf. III. Fig. 4, Cucurbita.)

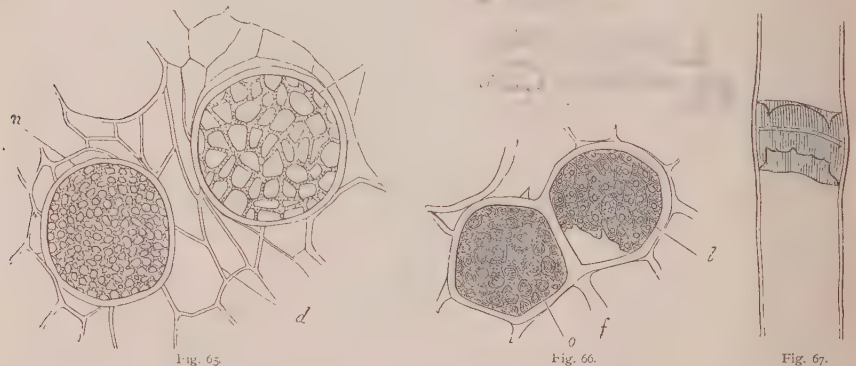


Fig. 65. Fig. 66. Fig. 67.

FIG. 65—67.—Lagenaria vulgaris, mature internode of stem (375). Fig. 65 and 66, transverse sections through one and the same bundle of sieve-tubes (or vascular bundle); *m* wide-meshed sieve-plate, occupying the whole horizontal end of a member, exposed, in surface view; *n*, *a* similar one with narrow pores, *l* another, injured at one margin in cutting the section, callous, the pores still slightly open; the original cellulose sieve recognisable through the callus; *o* sieve-plate covered by the contents coagulated with alcohol; *d* delicate parenchyma. Fig. 67, lateral view of two members of a sieve-tube attached end to end, the plate callous, so as to close the pores completely, the original sieve is recognisable in the middle between the two masses of callus.

According to the developmental data to hand, which however are not extensive on this question, the above-described simple structure makes its appearance on all sieve-plates on their first development. Many retain it long, or even throughout life; others alter, by assuming the condition termed by Hanstein *callous*[1]. The change consists in the thickening of the bands of membrane in all directions. They swell perpendicular to the surface to three or more times the original thickness, and become convex on their inner side: in the direction of the surface they expand so that the original pores are contracted to narrow cylindrical canals, which widen out like funnels only between the convexities of the inner surface. The single bands of membrane of one plate often take a different share in the callous thickening: this increases or decreases gradually on one plate from the middle towards the edge; in this matter both sides may be alike, or the reverse: the general form of the callous plate may thus be biconvex, biconcave, or plano-convex, &c. Often the inequalities of thickening are irregularly distributed over one face. The callous thickening may lastly extend in the direction of the surface so as to close the canals completely. Sieve-plates may often be found covered with a thick mass of callus, which is not perforated,

[1] [On the Callus compare Russow, Botan. Zeitg. 1881, p. 723.]

and in which the canals are only indicated by transverse striæ, and by funnel-shaped depressions of the surface: in others even these indications are not noticeable (Fig. 67, 76).

The callous plate always consists of three lamellæ, one central, and two applied to this laterally, one on each side: each of these belongs to one of the members of the tube. The middle lamella is the original cellulose sieve. The lamellæ of callus are in the fresh condition homogeneous, colourless, apparently soft, and having by transmitted light the peculiar bluish lustre of gelatinous membranes: they are coloured yellow by solution of iodine in potassium iodide, and by Schultze's solution a deep brownish-yellow: in sulphuric acid they swell till their outline is completely lost. A similar swelling results from the action of alkalies, especially solution of potash, and of Schultze's mixture. By these reagents the callus mass may be completely removed from the persistent cellulose sieve.

At the margin of the sieve-plate, next the adjoining membrane, the callus mass stops rather abruptly.

From all these phenomena it is concluded that the callus mass is formed by apposition upon the original cellulose sieve. The conditions of its appearance and its physiological significance require further investigation: according to some few experiments on Cucurbita and Lagenaria, the callous thickening seems in these cases to appear and increase with the age of the sieve-tubes, and in the first-formed (peripheral) tubes of a vascular bundle it seems to advance very quickly till the sieve is entirely closed. In many plants sieve-tubes may be found side by side without callus, and with callus in the most different stages, e. g. Lagenaria: in others, e. g. in the bast of Quillaja, only callous sieves are known, but they are always open. In the bast of many ligneous plants — Vitis, Tilia — I find all the sieve-plates completely closed by callus in the winter time; in the height of summer they are open and not callous. (Comp. Figs. 69, 74, and 76.)

The sieve-plates are always placed on the terminal faces of the cylindrical tubes. If these faces are horizontal, or only slightly inclined, each has throughout the properties of *one* sieve-plate, which may be termed a simple transverse plate: this is so in all the above-named cases of the original vascular bundles and primary bast of Angiosperms (comp. Figs. 65–67), in the slightly inclined terminal faces of Calamus, in the secondary bast of Fagus and Quillaja.

FIG. 68. — Cucurbita Pepo; mature internode, longitudinal section, parts of two sieve-tubes, with large callous plates at their terminal faces. The contents of both contracted by alcohol, but attached to the plates, and passing through the pores from one member into the other.

On strongly-inclined terminal faces the sieve-plates are arranged like the scalariform openings of vessels in series one above another, and are, like these, separated from one another by narrow bands of membrane: they usually form a single series, rarely they form here and there several irregular rows. Examples of this are supplied

by the above-mentioned secondary bast of ligneous Dicotyledons, e. g. Phytocrene, Bignonia, Tilia, Juglans, Vitis (Figs. 69–70), Betula, Populus, Pirus communis [1], &c., the very oblique terminal faces of Calamus (Fig. 71), Philodendron Imbe, &c. In the secondary bast of Vitis the occasional horizontal ends of members have also a ladder-like structure.

Sieve-plates are distributed in different ways, according to special cases, on the lateral faces of members of tubes, where these adjoin other similar members.

On most forms with simple transverse plates, as Cucurbita, they are not uncommonly absent on the sides, or they occur irregularly, and are then usually

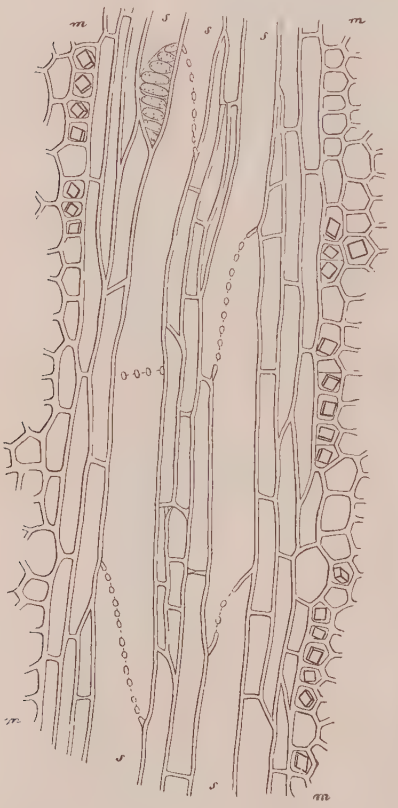


FIG. 69.

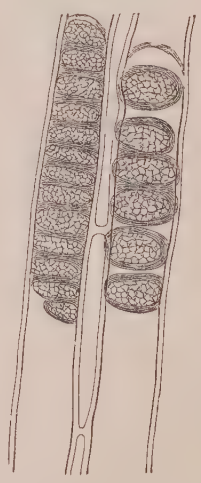


FIG. 70.

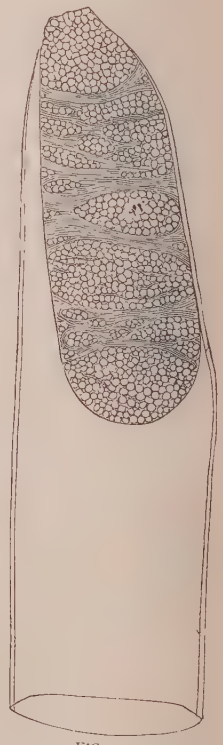


FIG. 71.

FIGS. 69, 70.—Vitis vinifera, Bast of a branch several years old, 1^{cm} in thickness, in Summer (beginning of July). Fig. 69 (145) Tangential section. *s*, *s* sieve-tubes, the inclined terminal surfaces, and a horizontal scalariform one, are cut through longitudinally, with the exception of one at the upper edge, which is seen obliquely in superficial view. *m*, *m* medullary rays, Fig. 70 Radial section, two scalariform terminal surfaces of sieve-tubes in superficial view, separated from one another by narrow parenchymatous cells (375).

FIG. 71.—Calamus Rotang (Spanish Reed). End of a member of a sieve-tube isolated by maceration (375).

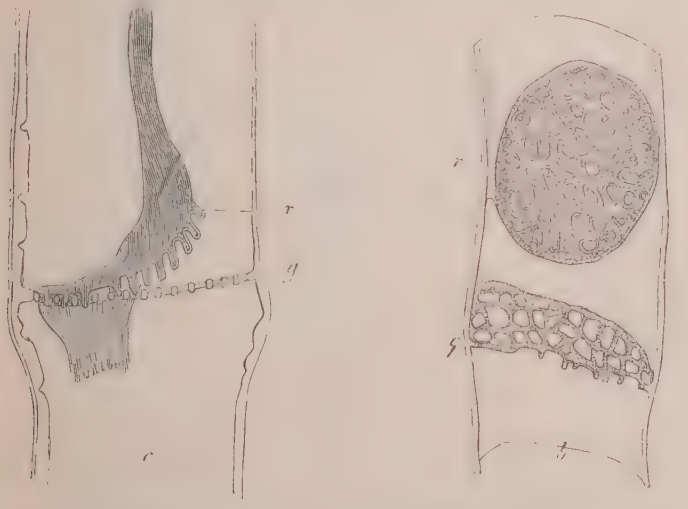
relatively small. Where the lateral wall adjoins elements of another category isolated, usually flat, pits are found: in these forms especially the lateral wall is very soft and extensible; after maceration in potash its inner layer may be drawn out to some

[1] Compare Von Mohl, *l. c.*; Dippel, Mikroskop, p. 251, &c.—Von Mohl's fig. 11 of Pirus represents the partial surface-view of three oblique terminal faces.

length. Among these forms the tubes of the secondary bast of Ficus elastica and Fagus sylvatica appear to be exceptions, since in them the lateral faces, turned towards the periphery and middle of the stem, are covered thickly with sieve-plates, which are only separated from one another by narrow fibre-like bands[1]. These plates on the lateral walls are extremely delicate, and it cannot be determined whether they really have pores, or are only portions of the wall having the latticed appearance of sieve-plates.

In the tubes with ladder-like terminal faces the series of plates is continued, usually quite gradually, from these to the neighbouring lateral surfaces, and especially on to the radial ones: in the bast of the Dicotyledons the arrangement is always such that the plates on the lateral surfaces are smaller and wider apart than on those which are terminal.

The contents of the fresh intact sieve-tube as it lies in water appear as trans-

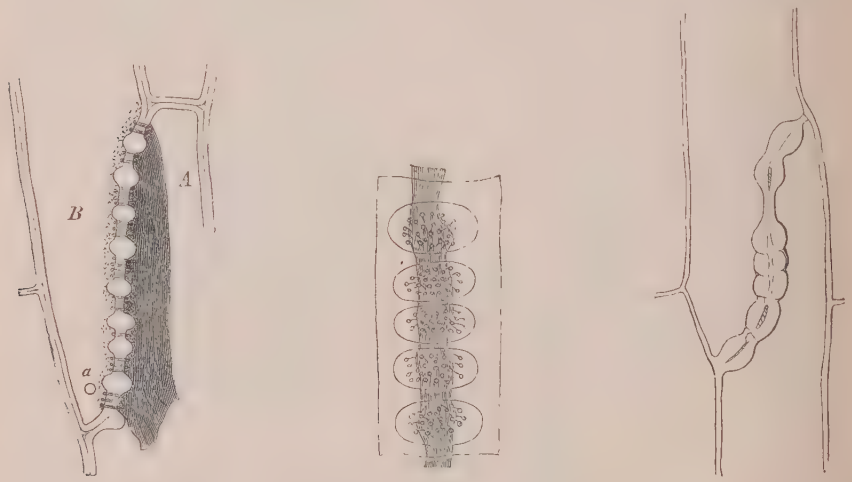


FIGS. 72, 73.—Two large sieve-tubes of Lagenaria vulgaris in longitudinal section, where two members join, after action of alcohol and iodine solution. In Fig. 72 *g* is the non-callous widely-perforated horizontal plate, as seen in longitudinal section; *r* the contracted sac-like contents, with the dense aggregation of slime. Processes from this traverse the pores on the left side; on the right side (*r*) they have been torn out of these in cutting the section. In fig. 73 the transverse plate (*g*) is oblique; thus the half of it present in the preparation is seen in section, and obliquely in surface-view. The coagulated slimy contents have been quite separated from it in cutting the section, and the plate, which rested on it, has been so turned that its whole surface, which before abutted on the intact sieve-plate, is turned towards the observer. The processes, which before fitted into the pores, appear upon it as rings (375).

parent as water. More exact investigation shows that the wall of each member of the tube is invested by a continuous thin layer of almost homogeneous slimy substance resembling protoplasm. This layer surrounds a central watery fluid, to which must be ascribed the alkaline reaction[2] characteristic of the contents of bundles of sieve-tubes, at all events in Cucurbita. At one end, or more rarely at both ends, of the member it encloses an apparently dense lustrous aggregation of slimy substance, which lies upon the sieve-plate, either as a thin lamella, or as a plug of relatively considerable

[1] Von Mohl, *l.c.*; Dippel, Mikroskop, p. 255.
[2] Compare Sachs, Botan. Zeitg. 1862, p. 257.

height. Usually this aggregation of slime is found at *one* end only of the member, and in that case, in Cucurbita according to Nägeli, in $\frac{4}{5}$ of the instances (taking the whole plant into consideration) it is at the *upper end*, that is, on the under surface of the sieve-plate. In very many cases numerous very small grains of starch are imbedded in the slime, and especially in the terminal aggregations of it [1]. Briosi found these in the stems and leaf-stalks of 129 out of 146 species investigated. At the sieve-plates the slimy contents are continuous through the pores from one member of the tube into the adjoining one. It may be seen, especially in callous plates, and when coloured yellow with iodine, filling all the pores and demonstrating, like a natural injection, the open communication through them (Figs. 68, 74). Where however the size of the parts makes an exact investigation possible, it may be seen that it does not pass as a homogeneous mass equally from one member into the



FIGS. 74, 75.—Vitis vinifera, Bast; from the same branch as Fig. 69, prepared on the same day (600).

FIG. 74.—Tangential section through the ladder-like limiting surface of two members of a sieve-tube *A* and *B*. In *A* the dense plug of slime, contracted by alcohol, sending blunt processes through all the sieve-pores into *B*; *a* a grain of starch.

FIG. 75.—Radial section, after action of absolute alcohol, destruction of the starch by brief action of strong solution of potash (the latter has caused a slight swelling of the membrane), and subsequent washing out of the potash, and treatment with iodine. Part of a ladder-like wall in surface view; beneath it the shrunken slimy contents of an adjoining member, which sends capitate processes—upwards as the preparation lies—through the pores into the other member.

FIG. 76.—Bast from a branch several years old, and 1·5 cm thick, of the same plant in winter. Callous closed wall between two members of a sieve-tube, tangential section (400).

other, but that the peripheral layer of the one member sends processes into the pores, which they fill, and ends blind at the limit of the adjoining member: the processes either end simply at the surface of the sieve-plate, or are more or less swollen, and rise above it into the cavity of the adjoining member, while at the point of transit through the plate they fit into corresponding holes in the peripheral layer of the member, which they enter (Figs. 72–75). As far as is at present known the processes always extend on one sieve-plate to one side only, thus from the member *a* to *b*, and not also conversely: further, they extend from the surface on which there is the larger collection of slime to the other. They are in their turn also filled with slimy contents. According to Briosi's statement, that the starch-grains often stick in the

[1] Briosi, Ueber allgemeines Vorkommen von Stärke in den Siebröhren, Botan. Zeitg. 1872, p. 305.—Compare also Sachs, Exp. Physiol. p. 383, &c.

sieve-pores, they must often also include starch-grains. This requires more exact proof. The starch-grains are doubtless densely crowded on the sieve-plate, and especially so on the pores. But they cannot so easily and generally enter and pass through the pores, since they are often larger than these: for instance, in Vitis, at the period of most active vegetation, they are on the average twice as broad as the pores. (Fig. 74, *a*.)

The structure described above is found in fresh intact sieve-tubes. But it appears much more plainly after the action of reagents. On treatment with alcohol the peripheral layer, resembling protoplasm, immediately coagulates along the sides of the members, separates from the membrane, and contracts to a relatively thin, folded, but still closed sac, which occupies the middle of the member (Figs. 68, 72, 74). On the face which is in contact with the sieve-plate, and which is attached by the processes in the pores, the sac retains its original width, or at least that of the perforated part of the wall: it thus widens more or less rapidly in a conical manner opposite these faces: the processes which enter the pores alter their form and position but little or not at all.

Iodine preparations produce the same changes in form, and colour the whole peripheral layer and the terminal aggregations of slime deep yellow to yellowish brown; the starch-grains violet[1]: this coloration appears much more quickly in the parts in question than in the callus-masses, so that by this means these two parts may easily be distinguished from one another: this renders the understanding of the structure more easy, especially in slightly-thickened and widely-porous sieve-plates, inasmuch as in this case the figures of the sieve-plates on the one hand, and on the other of the plates of slime (with their processes), which cover the sieve-plates, are necessarily similar in the surface-view of the plate, and are often difficult to distinguish at first sight. According to the above behaviour with alcohol, and preparations of iodine, and other known chemical reactions[2], the slimy contents of the sieve-tubes, i.e. both the lateral peripheral layer and the terminal aggregations, consist in the main of an albuminoid substance similar to protoplasm. It is doubtful whether it should really be termed protoplasm, less because of the slight differences between the iodine reaction of the slime and of the protoplasm of the surrounding tissue in Cucurbita[3], than because protoplasm is a body which is characterised not only by its material composition, but also by a definite organisation or structure, which expresses itself in protoplasmic movements, differentiation of nuclei, &c., and since phenomena such as the above have not been observed in the contents of sieve-tubes.

Sect. 44. In the *Gymnosperms* and *Fern-like plants*[4] tubes are found, in similar places to the sieve-tubes of the Angiosperms, which, from their great similiarity to these, are doubtless rightly included under the same term, but differ in certain points from them, and especially in the character of their contents.

The sieve-tubes of those *Gymnosperms* which have been investigated—e.g. Larix, Abies pectinata, Juniperus, Sequoja gigantea, Salisburia, Ephedra, Gnetum, Encephalartos—are similar in form and average size of the members to those commonly found in the bast of ligneous Dicotyledons, which have the ends of the members

[1] Compare Briosi, *l.c.* [2] Compare Sachs, Flora, 1863, p. 38. [3] Nägeli, *l.c.* p. 16.
[4] [See Janczewski, *l.c.*; also Russow, *l.c.*, and Strasburger, Zellhäute, p. 57.]

bevelled like a chisel. They may, like these, attain a considerable width, e.g. 0.030mm in the secondary bast of old roots of Abies pectinata. The oblique terminal faces are directed, both in the stem and in the roots, towards the radial planes (medullary rays). Sieve-plates are distributed uniformly in one or two longitudinal rows over the terminal faces, and the whole remainder of the radial lateral face. They form roundish spots, separated by high intervening portions, or are rarely elongated transversely, and separated by narrow ring-like bands: these spots are coarsely latticed, while in the cavities of the coarse lattice the very delicate sieve-structure is seen (Figs. 77, 78). Considering their close similarity to like parts of Dicotyledonous plants, there is no reason to doubt that the channel through the narrow sieve-pores is open. But this has not been directly proved, and the proof has hitherto been impossible, since the tubes in the plants in question are filled almost exclusively with watery fluid. The masses of starch-containing slime, giving the reactions of protoplasm, which in the Dicotyledons send their processes through the sieve-pores, have not yet been discovered in the plants in question: on the walls of the tubes there are attached internally some few very small granules, which turn yellow with iodine. The nature of the materials composing the fluid contents requires further investigation. Further, I was unable to find a formation of callus, with the exception of a doubtful case in the root of Abies pectinata.

FIG. 77.—Sequoja gigantea. End of a member of a sieve-tube, from the bast of an old stem, presenting the radial face. The uppermost (radial) wall is shaded. On it are small grouped sieve-plates with very fine pores, indicated only here and there by points (375).

Among the *Ferns* a number of plants have relatively large and wide vascular elements, and among these such as are, from their position (comp. Chap. VIII), and their structure, to be enumerated among sieve-tubes. This is the case in many Polypodiaceæ, e. g. Pteris aquilina (Fig. 79), Marsiliaceæ (Marsilia Drummondi and its allies), Cyatheaceæ, Osmundaceæ, Ophioglosseæ, according to Dippel in the Equiseta, and at least the larger Lycopodia[1].

In the Equiseta and the Ophioglosseæ they consist, according to Dippel and Russow, of tabular prismatic members, which stand one upon another in longitudinal rows with horizontal, callous, sieve-like, transverse walls. The lateral walls have no sieve-pits.

In the other cases cited, the members of the tubes are fitted one on another with pointed ends (in Marsilia also with horizontal ones), and have sieve-plates both on the latter, and also on the whole of those lateral surfaces which are contiguous with similar elements. These are usually elongated transversely, forming, according to the width of the surface of wall, one or several rows: in these rows they are either crowded closely, and separated only by narrow bands of wall (Fig. 79, *B*), or they are at a considerable, and then usually a variable distance from one another. The sieve-

[1] Dippel, Bericht d. 39. Versamml. deutscher Naturforscher zu Giessen, 1864, p. 146, Taf. IV. —Idem, D. Mikroskop, pp. 195, 203.—Russow, Vergl. Unters. pp. 5, 101, 118, 129, 142.

plates are not callous. Their pores, as far as they can be recognised, are very narrow and round; and in Marsilia, according to Russow, very numerous on one plate; in the cases investigated by me (Pteris aquilina, Cyathea, Alsophila spec., Osmunda) they are less numerous, and relatively far distant from one another. The wall of the tubes is thin at the sieve-plates; the rest of it is strongly thickened, stratified, and soft, and apparently swells in water. These tubes contain a quantity of watery fluid, and a thin peripheral layer, coloured yellow by iodine, which contains throughout, and especially at the ends of the members, and on the lateral sieve-plates, numerous very small granules which adhere closely to the wall. In dried-up tubes the ends are also found filled with a homogeneous brown mass. These granules are not starch: they turn a deep yellow with preparations of iodine: maceration in dilute solution of potash destroys them only partially even after many days. Their dense aggregation and their tenacious hold on the sieve-plates usually prevents a clear decision on the permeability of the pores: but I believe that I have clearly seen in thin longitudinal sections in Pteris aquilina that the granules of contiguous sieve-tubes are connected by thin filamentous processes which traverse the transverse pores (Fig. 79, *c*).

FIG. 78.—Encephalartos pungens. Bast of an old stem. Part of the radial wall of a sieve-tube (375).

The tubes are not inferior in width to the medium and thicker tubes of the Gymnosperms. The length of the single members is considerable, in the cases investigated (Pteris aquilina, Cyatheaceæ) it is 1–3^{mm}. In the Marsilias they attain, according to Russow, the length of one whole internode, that is, of several centimetres, a statement which may have its origin in the ease with which the ends of members may be missed in tubes prepared free by maceration.

In the larger indigenous Lycopodia (L. clavatum, annotinum) there occur in the vascular bundles of the stem organs which, in their position and width, have great similarity to the members of sieve-tubes of the above Ferns. They are prismatic and elongated, so that their pointed ends can seldom be seen in sections. Their contents correspond also to those of

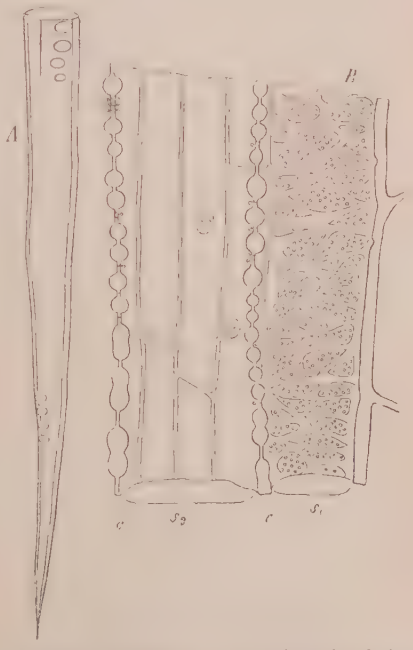


FIG. 79.—Pteris aquilina, Rhizome. *A* end of a member of a sieve-tube, isolated by maceration (144); *B* part of a thin longitudinal section. Thus has approximately halved two sieve-tubes, *S*1 and *S*2, which are so drawn, that the plane of section faces the observer, and the uninjured side lies behind. The latter is represented as lighter, while that which lies in the plane of section is darker. *S*1 abuts to the right on parenchymatous cells which have been cut through, to the left on *S*2; at the back again, its broad surface covered with sieve-plates, is contiguous with a sieve-tube, while to the left and at the back it abuts with a smooth wall on parenchymatous cells. *S*2 behaves with its whole smooth walled posterior side on parenchyma (the nucleus is indicated in two of the cells), right and left on sieve-tubes; *c*, *c* sections of walls bearing sieve-pits (375).

sieve-tubes. Neither Hegelmaier[1] nor I could find the clearly-latticed sieve-plates, almost like those of Pteris aquilina, which Dippel described on their lateral walls. On the other hand I saw on the whole lateral wall numerous small pits, solitary or in groups, to which were attached those peripheral granules, like those of Pteris aquilina, which turn yellow with iodine: but from these it could not be determined whether there are open sieve-pores or not (comp. also Chap. VIII). In the smaller Lycopodia, the Selaginellæ, and in very many Ferns with small vascular bundles composed of narrow elements (comp. e. g. below, Fig. 160, Polypodium vulgare), the position in which the sieve-tubes occur in the above instances is occupied by elements of similar form, and general character of contents and walls, but without distinct sieve-plates or sieve-pores. Whether the latter are really absent, and whether these elements are only the morphological equivalents of sieve-tubes, remains to be further investigated both in these cases and also in Lycopodium. I am the less inclined, in the doubtful cases, to deny the presence of sieve-tubes, and prefer the more to treat the question as an open one, because these very organs counsel one to be circumspect, for twenty-two years ago no botanist, with the exception of Hartig, had any idea of the characteristic structure of the most conspicuous of them.

[1] Botan. Zeitg. 1872, p. 778.

CHAPTER VI.

LATICIFEROUS TUBES.

Sect. 45. Certain plants, belonging to families or genera to be named below, known as plants which produce milk on injury, contain, in tubes of definite structure and of definite mode of development, a milky opaque fluid, which bears the name of *latex*; after this the tubes themselves may be called *Laticiferous tubes*[1].

The tubes traverse the parts continuously for long distances, adjoining more especially the turgescent, usually parenchymatous elements. They are themselves completely filled with the milky fluid, their walls, though often strongly thickened, are always soft, and easily compressed. Thus if a tube be injured at any point, the pressure exercised by the adjoining turgescent tissues forces the milk out through the opening.

The wall of the milk-tubes is always a soft, apparently watery cellulose membrane, which readily shows the characteristic blue coloration with preparations of iodine. Details of its structure will be given below.

Within the wall neither protoplasm nor nuclei are to be seen[2]. It is true many forms of coagulated, finely granular latex, e. g. that of the Cichoraceæ, resemble coagulated protoplasm, or there remains here and there, in partially emptied tubes after action of alcohol, solution of iodine, &c., a coat which looks like a coagulated protoplasmic lining to the wall. Further investigations will therefore perhaps be able to prove the presence of a protoplasmic body. Still, as it is difficult to obtain sharp anatomical evidence of such a body, and as our present knowledge both of the physiology and chemistry of latex is scanty, we may regard the contents as being fluids.

As the name implies, all latex consists primarily of a watery, in itself transparent fluid, in which numerous undissolved small bodies are suspended as an emulsion. In most cases both parts, the fluid and the bodies, are colourless, and the milk white: more rarely the milk is orange-red (Chelidonium), or sulphur-yellow (species of Argemone); but it is not possible to define exactly in these cases what share each of the parts takes in the coloration.

The clear watery fluid contains, as is shown by analyses of those sorts of latex which are used technically, very various bodies in solution; others, as indicated by the phenomena of coagulation, in a highly swollen state. In these two forms there generally occur in latex, varieties of gum, sugar, small quantities of albumen, often Pectic

[1] Milchsaftgefässe, Vasa lactifera, lactea, or Lebenssaftgefässe, Vasa laticis of authors.

[2] [On this point compare the papers cited below by Treub, Scott, Bower, and Schmidt.]

bodies (said to occur, e.g. in species of Lactuca), further tannin in many plants, especially the Aroideæ, Musa, also in the Cichoraceæ, and Euphorbia Lathyris: peculiar constituents soluble in water are found in many sorts of latex used officinally in the dry state, as e.g. morphin combined with meconic acid in opium; and lastly, the greater part of the ash which appears in analyses. As regards the form in which the latter occur in the living plant it should be mentioned that salts of malic acid, especially malate of lime, occur in very large quantity in the latex, at least of many Euphorbias. In the officinal Euphorbia (E. resinifera, Berg) the latter salt is found in large quantity: in the latex of one-year-old plants of E. Lathyris it occurs in autumn in so large quantity that when a drop of latex escapes into the air it immediately precipitates innumerable crystals [1].

As soon as latex comes in contact with the air, and still more quickly on treatment with water, alcohol, ether, or acids, coagula appear in the hitherto apparently homogeneous, clear fluid itself, and independently of the aggregation of the insoluble bodies, described by Mohl (Bot. Ztg. 1843, No. 33). The coagula collect together, and separate with the insoluble bodies from the clear fluid. These phenomena of coagulation, which appear under the action of so various agencies, point especially to a complicated composition of the fluid, and deserve further investigation.

The suspended bodies are present in the fluid in varying quantity, and the cloudiness of it is also variable, according to the age of the part, and according to the species: e.g. Morus, Nerium, and Stapelia show slight cloudiness; most species of Ficus and Asclepias have dense white milk. Excepting the starch-grains of the Euphorbias, which will be described below, the bodies have the form of round granules. They are in most cases—e.g. Euphorbia, and all plants with reticulate tubes—immeasurably small, and, when in free drops, they show active Brownian movement. The latex of the Artocarpeæ and Moreæ shows larger granules. They have in Ficus Carica an average diameter of 3μ (1.4μ to 5.6μ), and show concentric stratification, as found by Caruel [2], the larger having three layers of almost equal thickness surrounding a small nucleus, the smaller only two layers. The outermost layer is sharply distinguished by different refrangibility from the inner ones. The granules of the latex of Ficus elastica, Broussonetia papyrifera, Maclura aurantiaca, have in the main the same structure; also, though less distinctly, the very variously sized ones of Morus nigra: all these granules are soft and sticky, and readily adhere and collect together after leaving the plant.

The slightly milky latex, which escapes from young petioles of Nerium Oleander, contains pale, apparently homogeneous, spherical bodies of unequal size, two or more of which are often adherent to one another: the larger of these exceed those of the Fig. in size. Much larger spheres are described in the case of Musa.

On the chemical nature of the granules the existing chemical analyses tell us that —leaving out of account relatively very small quantities of substances characteristic of special cases, such as the alkaloids of Opium, which are insoluble in water—they may be generally designated on the one hand as resins, on the other as consisting of

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[1] The chemical definition of the crystals I owe to the kindness of Professor Flückiger.

[2] Sur les granules particuliers du suc laiteux du figuier, Bull. de la Soc. Bot. de France, XII (1865), p. 273.

Caoutchouc. There are also found relatively small quantities of fat, and wax-like bodies: of the latter a large quantity is described only in Galactodendron (Solly's Galactin). Resins are abundant, e.g. in the Euphorbias, and in Opium. Caoutchouc, on the other hand, is stated to exist in the latex of very numerous species, belonging to the most various families of Dicotyledons. It forms sometimes the large majority of the constituents which are insoluble in water, as in the Euphorbiaceæ (species of Hevea), Artocarpeæ (species of Ficus, Castillea), Apocynaceæ (species of Haucornea, Urceola, Landolphia, Vahea), which yield the Caoutchouc of commerce, to which, according to existing statements, might be added the Asclepiadaceæ (Calotropis gigantea) and Lobelia Cautschuk[1]. In other cases, according to certain unreliable statements, it occurs in small quantities in many sorts of latex, e.g. in that of Lactuca virosa and Papaver somniferum. It is still uncertain whether the constituent described as Caoutchouc or 'india-rubber' is universally the same chemically distinct body. Further, it is uncertain whether the body or bodies included under this name are the sole constituent of the granules of latex, or whether these each consist of a mixture of different substances. The above-mentioned differentiation of the granules of Ficus, which certainly consist chiefly of Caoutchouc, into layers of different refrangibility, makes the latter view more probable in this case.

Besides the bodies described, there are found in the latex of the Euphorbias numerous starch-grains[2]. In the herbaceous (Tithymalus) species they are usually of the form of cylindrical or spindle-shaped rods, which in E. Lathyris grow to 55μ in length, and 10μ in thickness, in E. Cyparissias to 40μ in length, and 6μ in thickness; more rarely they have a roundish form, or (especially in E. Myrsinites) rather swollen ends. In the shrubby and succulent species of hot latitudes they are shaped like a flattened rod, and appear from the narrow side linear-spindle-shaped; seen from the broad side they show a massive broad central part, and much widened, roundish spatula-shaped, often lobed ends[3]. Also in others but by no means all of the Euphorbiaceæ rod-shaped starch-grains occur in the latex: e.g. spindle-shaped ones in Excæcaria sebifera, Müll., staff-shaped in Hura crepitans[4]. How far the blue coloration, which Hartig[5] saw appear with iodine in glycerine in the latex of Chelidonium, and which Trécul[6] saw with iodine in that of Nerium, Cerbera Manghas, &c., after boiling with potash, arises from very small starch-granules, remains to be further investigated.

The above observations, compiled from data at hand, will show sufficiently well how little is known for certain of the anatomy of latex, which has been entirely neglected since Mohl's work of the year 1843, and how much may be expected from renewed investigation. The same holds with regard to the chemical conditions. A number of investigations have been made in this direction on sorts of latex, such as Opium, Euphorbium, &c., which are used technically or medicinally, without giving any

[1] Compare on the plants which yield Caoutchouc, Collins, Report on the Caoutchouc of Commerce, London, 1872; Wiesner, Rohstoffe des Pflanzenreichs, p. 153.

[2] Rafn (Pflanzenphysiol. p. 88) first noted them; they were first recognised as starch by T. Hartig, 1835; Erdmann and Schweigger-Seidel, Journ. f. pract. Chemie, Bd. V. p. 4.

[3] Compare Meyen, Physiol. *l.c.*; Nägeli, Stärkekörner, p. 428; Weiss und Wiesner, Botan. Zeitg. 1861, p. 41, 1862, p. 125.

[4] Vogl, in Pringsheim's Jahrb. V.

[5] Botan. Zeitg. 1862, p. 100.

[6] Comptes Rendus, tom. LXI (1865), p. 156.

ground for deciding upon the possible chemical changes which result from drying in the air. Reference must be made to the technical, and especially the pharmacological literature, for information on the above-mentioned investigations[1]. Here only some few results may be given of analyses of fresh specimens of latex, or of such as were kept so as to prevent drying up, by way of giving a rough idea.

Faraday[2] investigated the latex of a rubber-tree of the family Euphorbiaceæ—'Hevea elastica, Siphonia elastica, Pers.,' probably H. guyanensis—which had been sent to England in closed bottles. The fluid contained in 1000 parts—

Water with an organic acid	563
Caoutchouc	317
Albumen	19
Bitter substance (with much nitrogen) and some wax	71·3
Bodies insoluble in alcohol, soluble in water	29·1

The preserved latex of Galactodendron utile contains, according to Heintz[3], in 100 parts—

Water	57·3
Albumen	0·4
Wax ($C_{35} H_{66} O_3$)	5·8
Resin ($C_{35} H_{58} O_2$)	31·4
Gum and Sugar	4·7
Ash	0·4

Weiss and Wiesner[4] investigated the fresh latex of some indigenous Euphorbias. In the slightly acid latex of E. Cyparissias they found in 100 parts—

Water	72·13
Resin	15·72
Gum	3·64
Sugar and extractives	4·13
Albumen	0·14
Ash	0·98

For comparison with these may be given the composition, as found by Flückiger[5], of Euphorbium, *i.e.* the fixed residue of the latex of E. resinifera—

Amorphous resin ($C_{20} H_{32} O_4$)	38
Euphorbon ($C_{26} H_{44} O_2$)	22
Mucilage[6]	18
Malates, especially of calcium and sodium[7]	12
Other constituents of ash	10
	100

Sect. 46. The tubes themselves, in which the latex is contained, are all alike in certain points of structure and arrangement, but may be divided, according to form and development, into two categories, *articulated* and *non-articulated* laticiferous tubes. Each of these categories is peculiar to definite families, the *articulated* tubes being

[1] Compare Wiesner, Rohstoffe des Pflanzenreichs; Flückiger, Pharmacognosie; Flückiger and Hanbury, Pharmacographia; Rochleder, Phytochemie, &c.; also Meyen, Physiol. II. *l.c.*

[2] Compare Berzelius, Jahresbericht for 1827 (German by Wöhler), p. 246.

[3] Poggendorff's Ann. 65 (1845), p. 240.

[4] Botan. Zeitg. *l.c.*

[5] According to Flückiger and Hanbury, Pharmacographia, p. 504.

[6] Probably inclusive of starch or its products of decomposition.

[7] Compare the former statement for E. Lathyris.

found in the *Cichoraceæ*, *Campanulaceæ*, *Lobeliaceæ* (and, according to Trécul, in Gundelia Tournefortii, one of the *Cynaraceæ*), the *Papayaceæ*, many *Papaveraceæ* (Papaver Roemeria, Argemone, Chelidonium, but not Glaucium, Macleya, Sanguinaria), many *Aroideæ*, and *Musaceæ*. The *non-articulated* tubes are found in the *Euphorbiaceæ*, *Urticaceæ* in the wider sense (including the Artocarpeæ, and Moreæ), *Apocynaceæ*, and *Asclepiadaceæ*.

The properties common to all are, firstly, that they traverse the whole length of the mature parts of the plants as continuous, and, with rare exceptions (Musa, Chelidonium), frequently-branched tubes; and not only do they traverse each single member of the plant on its own account, but they send branches from these into all the like and unlike lateral appendages.

Secondly, all laticiferous tubes have, as was above noted, soft, apparently very watery, smooth or flatly pitted cellulose walls, which often show the characteristic iodine reaction of collenchymatous walls (cf. p. 120). These are in many cases very delicate, and without recognisable minute structure: thus, e.g. almost universally in the Aroideæ, in Vinca, Asclepias curassavica, and in other cases in the thin branches of higher order. The membrane of the stronger stems and branches of most tubes is thickened, and appears as though swollen in transverse sections, having delicate stratification, while striation is also seen, especially in the strongly-thickened tubes of woody stems (species of Euphorbia, Nerium). The thickening increases with age. Even in the very thick membranes no sculpture of the surface can be recognised: on the other hand delicate transversely-oval pits are often seen, e. g. in the tubes of Plumiera alba, in those of the base of the stem of Campanula Medium (Trécul), and in old stems of Lobelia syphilitica. In the base of the stem of species of Argemone are found crowded together band- and knot-shaped thickenings which protrude inwards. The wall of the tubes of Plumiera alba may be split, according to Trécul, into spiral bands of 10μ–15μ in breadth.

Further, pits occur less commonly on the lateral walls than appears at first sight, especially in articulated laticiferous tubes, since the lateral wall of these, especially when old, has often very numerous and short protrusions, which give, in surface-view, the figure of pits with delicate contour. I could never find support for those statements, according to which the pits of the lateral wall have the structure of sieve-plates.

As will be more completely described in Chapter XII, but must here be only briefly stated, the laticiferous tubes permeate the whole body of the plant, in most cases as a continuous system, sending branches from the stem into all lateral members. These branches often push their way between the elements of all regions, and of all tissues of other sorts than themselves. As regards the main branches or stems of the tubes however it is generally the case that they follow the vascular bundles, i. e. the wood and bast, as concomitants of, or sometimes even substitutes for the sieve-tubes. In this course they often approach very closely in point of distance to Tracheæ, especially vessels, and on this circumstance, together with the above-mentioned (p. 169) occurrence of apparently coagulated latex within the vessels of laticiferous plants, depend the controversies on the anatomical relations between these two series of organs. The fact is that the tracheæ of the furthest ends of vascular bundles in the laminæ of leaves are often accompanied by branches of laticiferous

tubes, and are in immediate contact with these[1]: further, that in the xylem of the stem of the Papayaceæ the laticiferous tubes are directly and firmly attached to the large vessels, sometimes throughout their length, sometimes by single ends of their branches[2]: again, that a similar relation exists between the laticiferous tubes which accompany the vascular bundles of many Aroideæ and the tracheæ which belong to them[3]. Finally, it is an indubitable fact that in sections through plants having laticiferous tubes, numerous vessels are often to be found filled with coagulated masses, which appear very similar to the coagulated latex of the plant, and which also have its characteristic colour, e. g. in Chelidonium reddish yellow[4]. This latter phenomenon often occurs very conspicuously in roots, and under conditions which do not allow of the idea of a flow of the latex from a cut surface. Trécul concludes from this series of facts, observed by him in many cases, that in all plants with laticiferous tubes at least single branches of the tubes come into direct contact with tracheæ, and open communication is set up by perforation of single portions of the wall at the points of contact[5]. He even states that he has directly observed the points of perforation, e. g. in Lobelia laxiflora. Other observers, among whom I must place myself, according to my investigations up to the present time, have been unable to find such contact and communication of milk-tubes with the tracheæ, with the exception of the above-mentioned cases of the Aroideæ and Papayaceæ: on the other hand, they have seen that where branches of milk-tubes run from the cortex to the pith, they take a course by the medullary rays through the woody or vascular ring. Trécul's statements accordingly require further proof: in the first place, that on the general contiguity of milk-tubes and vessels, and secondly, that regarding the open anastomosis of milk-tubes into vessels, which should be confirmed in the case in which it was observed by him, and, at all events, in the Papayaceæ and Aroideæ. According to the present data these anastomoses occur very seldom, and it is extremely difficult to prove them with certainty by direct observation, and to distinguish them from non-perforated pits. If they do really occur, still it is not proved that they are proper to normal tissue, and not really pathological phenomena, i. e. ruptures in the thin places of contact of the tubes, which arise in the same way, through the pressure of the turgescent parenchyma, as the discharge of latex on surfaces of section. The apparent presence of coagulated latex in vessels is evidence at first sight of the existence of open pores: the normal existence of these is however made the more doubtful by the fact that, as far as investigated, the occurrence appears to be quite irregular and inconstant, and that milky or resinous coagula are found in vessels even in such plants as have no laticiferous tubes, but closed secretory cavities, without any open connection with the vessels.

If an anastomosis, or even a mere contiguity of milk-tubes with the tracheæ, does not occur in most cases, and I consider this most probable, there is then no explanation of the occurrence of what appears to be coagulated latex in the latter: for such an explanation it is however necessary, in the first place, to answer the question,

[1] Compare, e. g. Hanstein, Milchsaftgefässe, Taf. IX. fig. 13 (Lactuca virosa).
[2] Trécul, Ann. Sci. Nat. 4 sér. VII. p. 289, pl. 12 (1857); Comptes Rendus, tom. 45, p. 402.
[3] Compare Hanstein, *l. c.*; Van Tieghem, Structure des Aroidées, *l. c.* Taf. II. fig. 1, pp. 6–8.
[4] [Compare von Höhnel, Milchsaft in Tracheen, &c. *Ref.* Bot. Jahresbericht, 1878, I. p. 30.]
[5] Compare especially Comptes Rendus, tom. LX (1867), p. 78.

whether those coagula are really latex which came as such from the tubes, and not products of coagulation of fluids which had diffused through the walls of the vessels.

SECT. 47. The distinctions of the two categories of laticiferous tubes depend upon certain phenomena of their development and form. The *articulated* series, as types of which those of the Cichoraceæ, Papaveraceæ, and Papayaceæ may serve, arise from series of elongated cells of the meristem (or cambium), which coalesce, by perforation of their septa, to form continuous tubes. In the simplest case, which occurs in Musa and Chelidonium (Figs. 80, 81), the tubes remain simple, or are branched, and connected in a net-work only inasmuch as one series of their original members may

FIG. 80.—Chelidonium majus; tangential section through the secondary cortex of an old root; *m*—*m* and *b*—*b* portions of milk-tubes between the cells of the parenchyma. At *a*—*a* *m* passes *beneath* the parenchymatous cells (225).

FIG. 81.—Chelidonium majus; stem, cortex, radial section, part of a milk-tube with a perforated septum at *s* (225).

continue its course from any given point as two diverging series, and conversely. The septa between the original members are here perforated only in the middle by one or few holes; their margin is persistent; occasional large openings in the lateral wall also occur in rare cases, where two tubes are directly contiguous.

In the majority of really typical cases the septa between the members of each series soon disappear completely, so that in the mature tube no trace of them remains. Occasionally in such cases single septa may persist through life.

The tube puts out lateral protrusions, usually at numerous points, which force

themselves between the neighbouring unlike tissue-elements, and grow out to cylindrical branches, which sometimes remain short, not longer than broad, and sometimes attain a considerable length. Some of these protrusions end blind, others join with similar ones from neighbouring tubes, or with the trunks of these, and open communication is formed by disappearance of the wall at the point of contact. Where two tubes run longitudinally side by side, they are further directly connected by numerous large perforations of the wall of contact. Thus there arises a net of communicating tubes which is usually very complicated, with meshes of most various form and size, and with blind branches of various length and direction, imbedded in

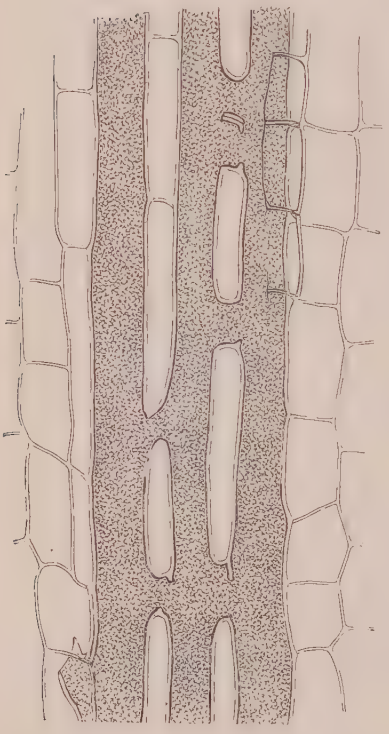

FIG. 82.—Tangential section from the cortex of Lactuca virosa, with three reticulately joined milk-tubes (225).

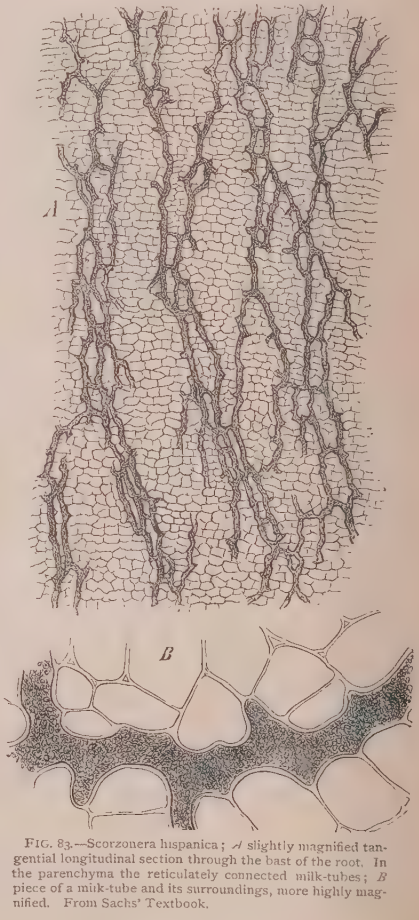

FIG. 83.—Scorzonera hispanica; *A* slightly magnified tangential longitudinal section through the bast of the root. In the parenchyma the reticulately connected milk-tubes; *B* piece of a milk-tube and its surroundings, more highly magnified. From Sachs' Textbook.

surrounding—usually parenchymatous—unlike tissue (comp. Figs. 82, 83). This network, as above stated, extends throughout the whole plant. Non-reticulate articulated tubes, such as those of Chelidonium, are branched, at least at the points of insertion of lateral ramifications, and send out branches from these points into the latter.

SECT. 48. The **non-articulated laticiferous tubes** do not show a net-like

anastomosis in any well-constituted case; all their branches, which are often very numerous, end blind (Fig. 84). Anastomoses may occur between their branches in the nodes of many plants (leafy Euphorbias), but this is quite uncertain. Each tube arises, not from a series of coalescing cells, but from one single cell of the meristem, which grows so as to form a long branched sac, and forces its branches between the other tissue-elements. The statements concerning their first development differ greatly. According to Schmalhausen's investigations on species of Euphorbia and Asclepiadaceæ, to be more fully stated below, some few cells of the meristem in the cotyledonary node of the embryo, outside the plerome, are the starting-points of the milk-tubes. These begin, even in the young embryo, to elongate into cylindrical sacs, and to penetrate with their growing ends between the neighbouring cells into the cotyledons and towards the end of the root: they have at an early stage occasional branches in the cotyledonary node. *All tubes* in the primary cortex, the leaves, and the pith of the mature plant are *branches of these few sacs, which are present in the young embryo.* From the embryonic stage onwards their ends extend to close (6–8 cells) beneath the primary growing points, and grow onwards with these, sending branches, which have the same properties, into the lateral buds, leaves, and roots, as soon as these make their appearance. Lastly, they branch further and elongate in the meristem and the young parts so as to form the final system of tubes. The whole plant, e. g. a shrub of Euphorbia the height of a man, has thus only few, much-branched milk-tubes, the ends of the branches of which extend on the one hand into all growing points, and grow with these to an unlimited extent, on the other hand they are distributed in the mature tissues in the manner described, and end blind. As a matter of fact pieces of tubes an inch long, with hundreds of branches, may be teased out of macerated portions of the stem without finding a single anastomosis, or any other blind ending than those of small lateral branches (comp. Fig. 84 *A*).

FIG. 84.—*A* part of a trunk of a milk-tube, with its stronger branches prepared free and spread out, hardly larger than natural size, from the stem of Euphorbia splendens. *All ends of which and to which are broken off.* *B* from the stem of Ceropegia stapelioides, terminal branches of a non-articulated milk-tube prepared free, with numerous blind ends of branches (145).

According to observed facts the *possibility* cannot be denied, that in later stages of development of a plant, especially in the nodes, single cells of the meristem develope into new milk-tubes, and may coalesce as branches with those which originate from the embryo. However, the occurrence of this phenomenon, if indeed it occurs at all,

is very restricted, and not clearly proved hitherto by any observation. I was unable, even in the milk-tubes, which are present in large quantities throughout the secondary bast of Morus, Ficus, Maclura, and Nerium, to prove that they arise successively afresh from the cambium (Chap. XIV), and are not branches of the original tubes which thrust themselves into the layers of secondary bast. A positive proof that the latter is the case has, it is true, not been as yet obtained.

The peculiarities of form and structure of milk-tubes in special cases of their occurrence will, in order to avoid unnecessary repetition, be described together with the treatment of their arrangement in Chap. XII.

The peculiar juice which flows from milky plants, and the peculiar tubes which contain it within the plant, were known to the fathers of vegetable anatomy, but without their having sharply distinguished them from the reservoirs of resin and other secretions, described in Sect. 34, and from the intercellular passages which so frequently have contents of similar appearance. The terms then in use, viz. Succi proprii, and reservoirs of such peculiar juices, referred rather to these latter forms of tissue and cavities, or to their contents[1]. After many more or less successful attempts to distinguish them accurately and separate them (the history of which may be found in Meyen and Treviranus), C. H. Schultz-Schultzenstein from 1823 onwards[2] drew the attention of his contemporaries to the tubes with which we are engaged, and earned for himself in his later works, especially two large publications in the year 1841[3], the merit at least of isolating by maceration the network of tubes of the Cichoraceæ, Campanulaceæ, and the tubes of the Euphorbias, &c., and drawing them for the most part correctly in their main points. It is true his works were rendered unpalatable by his terrible views on circulation, or, as he calls it, Cyclosis of the milk, or sap of life (Latex) in the 'Vasa laticifera,' and that which was really good in his observations was hidden by the mass of preposterous statements and representations into which he let himself be led by the idea that networks of vessels of sap of life must be universally present. Misunderstood sieve-tubes (the structure of these was quite unknown before 1837), fungal hyphæ (comp. Cyclosis, Taf. IV), and many objects which cannot be defined accurately from the figures, were confounded with real milk-tubes Almost simultaneously with these larger publications of Schultz, and in connection with them, Meyen[4] gave, on the whole, very good representations of the structure of a number of latex-tubes, but without giving any close attention to the most elaborate networks of tubes such as occur in the Cichoraceæ and their allies. The knowledge of the structure and distribution of the tubes was further advanced by Hanstein[5], Dippel[6], and other authors, to be named later, who have worked at their development; Hartig[7] having first sharply distinguished the articulated from the non-articulated forms, and Unger[8]

[1] Compare Treviranus, Physiol. I. p. 137, &c.; Meyen, N. Syst. d. Pflanzenphysiol. II. p. 371, &c.

[2] Ueber den Kreislauf des Saftes im Schöllkraut.

[3] Die Cyclose des Lebenssaftes in den Pflanzen, Nov. Acta Acad. Leopoldino-Carolin, vol. 18, Supplem. II. p. 336 S. 33 Taf.—Mémoire pour servir de réponse aux questions de l'Acad. des Sci. pour l'Année 1833; Mém. prés. à l'Acad. des Sci. tom. VII. p. 104 S. 23 Taf.

[4] Die Secretionsorgane der Pflanzen (1837), Physiol. II. pp. 376–386.

[5] Die Milchsaftgefässe, &c. Berlin, 1864.

[6] Entstehung der Milchsaftgefässe, Verhandl. d. Bataafsch. Genootschap. &c. te Rotterdam, tom. XII. p. 3 (1865).

[7] Botan. Zeitg. 1862, p. 99.

[8] Anatomie und Physiologie, p. 157.

having given a short and clear, though not quite correct review of the leading types. A great service in advancing the knowledge of these organs was further rendered by Trécul, who, in a series of papers published since 1862, described his very numerous observations, and thereby gave the impulse to the new works on the development of these organs. It is true Trécul[1] inclines again to the old idea of circulation, and places the milk-tubes nearer other reservoirs of 'sucs propres' than is allowable from an anatomical point of view.

Finally, Vogl[2] has supplied a number of valuable contributions and confirmatory observations.

The *history of the origin* of the milk-tubes, so indispensable to a clear understanding of their structure, remained long in the dark[3]. Unger's view[4], according to which (from observations on Ficus benghalensis) they arise from rows of cylindrical cells by coalescence, found no response, and opinions remained undefined, till in 1846 the often-mentioned anonymous writer in the Botanische Zeitung expressed the opinion, as the result of an extended series of investigations, that each milk-tube is originally an intercellular passage without a wall of its own, which is subsequently provided with a membrane peculiar to it, through the agency of the adjoining cells. The contradiction by Schacht[5] of this view, which was at first not unfavourably received, and the subsequent answer by Trécul, called forth the series of newer works, by which the anonymous writer was refuted, and a clearer knowledge of the matter was gained, at least in many particulars. Unger formulated his view afresh in 1855[6], in these words. The milk-tubes are 'shorter or longer, cylindrical, irregular or branched cells, filled with opaque milky or dark coloured juice, which fuse with one another in longitudinal rows or at their points of branching.' He lays

[1] From the series of Trécul's papers which treated of 'sucs propres,' those on milk-tubes may here be named: Des vaisseaux propres en général et de ceux des Cynarées laiteuses en particulier, L'Institut, 1862, p. 266.—De la présence du latex dans les vaisseaux spiraux .... et de la circulation dans les plantes, Comptes Rendus, tom. 45, p. 402 (1857).—Des laticifères dans les Papavéracées, Ibid. tom. 60, p. 522 (1865).—Sur les laticifères des Euphorbes, &c., Ibid. tom. 60, p. 1349.—Laticifères et liber des Apocynées et des Asclépiadées, &c., Ibid. tom. 61, p. 1349; L'Institut, 1862. p. 215.—Des laticifères dans les Chicoracées, Ibid. tom. 61, p. 785 (1865).—Des laticifères dans les Campanulacées, Ibid. p. 929.—Des vaisseaux propres dans les Aroidées, Ibid. tom. 61, p. 1163 (1865), et tom. 62, p. 29 (1866).—Matière amylacée .... dans les vaisseaux du latex de plusieurs Apocynées, Ibid. tom. 61, p. 156 (1865).—Rapport des laticifères avec le système fibro-vasculaire, Ibid. tom. 51, p. 871 (1860).—Rapports des vaisseaux du latex avec le système fibro-vasculaire; ouvertures entre les laticifères et les fibres ligneuses ou les vaisseaux; Ibid. tom. 60, p. 78 (1865).—Des vaisseaux propres et du tannin dans les Musacées, Ibid. tom. 66, p. 462 (1868).—Most of these works were reprinted in the Annales des Sciences Naturelles; all in Baillon's Adansonia, tom. VII–IX.

[2] Ueber die Intercellularsubstanz und die Milchsaftgefässe in der Wurzel des gemeinen Löwenzahns, Sitzungsbr. d. Wiener Acad. Bd. 48.—Beiträge z. Kenntniss der Milchsaftorgane d. Pfl., Pringsheim's Jahrb. V.

[3] [On this subject see further Schmalhausen, Beitr. z. Kenntniss d. Milchsaftbehälter d. Pflanzen, Mém. de l'Acad. Imp. de St. Pétersbourg, XXIV. 1877.—Faivre, Compt. rend. hebd. t. LXXXVIII.—D. H. Scott, Development of articulated laticiferous vessels, Quart. Journ. Micr. Sci. 1882.—E. Schmidt, Botan. Zeitg. 1882, p. 435.—Treub, Comptes rend. 1 Sept. 1879, Archives Néerlandaises, t. XV].

[4] Annalen des Wiener Museums f. Naturgesch. bd. II (1840), p. 11, where it is attempted to adduce a proof, weak enough even for that time.—Endlicher u. Unger, Grundzüge (1843), p. 40.

[5] Botan. Zeitg. 1851, p. 513.

[6] Anatomie und Physiologie, p. 157.

special stress upon the coalescence of originally separate cells, since he places all milk-tubes among his 'cell-fusions,' and only cites as cases where the cells do not coalesce to tubes, those of Chelidonium, in which plant he overlooked the perforation of the septa, and those of Sanguinaria, which must be entirely excluded from the category of milk-tubes. All investigators acceded in the main to Unger's view. Dippel and Hanstein made thorough investigations, which proved it clearly for many cases (articulated tubes). Schacht had already published at an earlier date [1] an excellent history of the development of the tubes of Papaya from coalescing cells of the meristem, and greatly shaken thereby his own view repeatedly proclaimed since the above-cited work of 1851, according to which the milk-tubes are no special form of tissue at all, but only 'Bast cells,' i. e. sclerenchymatous bast fibres, filled with latex [2].

All the later authors mentioned, who expressed their views on the subject, extended the above theory of coalescence to all milk-tubes, both articulated and non-articulated. The first objections to this are to be found indicated by Hartig, but have recently been more clearly brought forward by David [3]. As may be seen in the above statements, the two sorts of tubes should be treated separately.

For the *articulated tubes* it can no longer be doubted, after the excellent descriptions of their development by Schacht, and particularly those by Dippel, that they arise, as above described, by coalescence of cells. Without the development having been traced step by step, this follows in the case of the tubes connected into a net from the fact that in an earlier stage there are only simple cells of the meristem in the position afterwards occupied by the network. The fact may be proved most clearly in the secondary cortex of the Cichoraceæ. In the tubes of Chelidonium, which are not connected into a network, the limits of the original cells remain partially preserved through life.

The *non-articulated* tubes offer much greater difficulties. Most authors since 1846 have simply extended to them the same history of development as was observed for the articulated tubes; only Dippel and David attempted to get to the bottom of the question by direct observation. Dippel followed the tubes, in Ficus Carica and Euphorbia splendens, into the youngest meristem of the growing point, and close to the latter he found here and there septa in the tubes: he found such septa also in occasional preparations of old tubes of Euphorbia Cyparissias, Asclepias curassavica, Nerium Oleander, and Vinca minor, and concludes from this that they arise by coalescence.

David arrived at a quite different result for the families named in the title of his dissertation, of which he investigated the following species specially: Euphorbia splendens, Caput-medusæ, Lathyris; Ficus elastica, Carica; Nerium Oleander, and Hoya carnosa. According to him each non-articulated milk-tube is one cell, 'a milk-cell,' originating at an early stage by the elongation of one single cell of the meristem, which branches, and thrusts itself between the elements of the surrounding tissue. All the branches of each of these cells end blind and closed: the cell may grow to a great

[1] Monatsbr. d. Berliner Academie, 1856, *l. c.*

[2] [F. O. Bower, on Gnetum, Q. J. M. S. 1882.]

[3] Ueber die Milchzellen der Euphorbiaceen, Moreen, Apocyneen, und Asclepiadeen; Dissert. Breslau, 1872.

length, in E. splendens, e.g. more than 12mm, in E. Lathyris, the length of an internode plus the leaf belonging to it, that is about 20 cm. As the plant grows, new milk-cells are formed in the growing point of the stem: the tubes of the leaves are only branches of those which traverse the stem. It is obvious that this view scarcely differs except in name from Schacht's theory of bast cells. David's chief proof of his statement was obtained by him by macerating sections of the apical meristem with potash, and then teasing out from them the young milk-cells, which are at first short and spindle-shaped, but gradually become elongated and branched. In non-macerated sections also he was able to find the required early stages. The examination even of the mature specimens shows that David's view is impossible, for, as above shown, the tubes, e.g. of the Euphorbias, can be followed for any distance, and numerous blind peripheral ends of branches may be found in leaves, cortex, and growing points, but never a completely closed tube which is of less length than the whole plant. Were the tubes originally formed in succession as single completely closed cells of the growing point, they must have coalesced with one another to form the mature tubes.

As a matter of fact those solitary spindle-shaped initial cells of the milk-cells do not exist. The tubes run continuously into the furthest meristem of the growing point, their ends can be followed to within 6–8 cells of the extreme apex: their course is variously curved both in radial and tangential direction between the developing parenchymatous cells; longitudinal sections must thus cut off portions of them, which are roundish, or spindle-shaped, or cylindrical, and look exactly like cells of such form, especially if the section be very thin and transparent, or if the delicate, very readily swelling membrane be swollen by maceration in potash. David's young milk-cells are such sections of tubes: they were represented by Dippel, but were rightly explained.

Dippel's view does not rest, like that of David, on mistakes of observation, which might easily be avoided: it is, from analogy with articulated tubes, extremely probable: still I was unable, though I investigated the matter repeatedly, with every prejudice in its favour, to find the view confirmed by observation. If one examines the ends of stems in species of Euphorbia, Stapelia, or Ficus, which are elongating, but before secondary thickening begins, the last ends of the tubes and their branches always extend, as has been repeatedly stated, into the furthest meristem of the growing point, and of its youngest leaves and branches, and I was never able to observe in their cavity traces of septa or of any coalescence of originally separate cells. Where septa appeared to be present in the young ends of tubes, and this was not rarely the case, continued and careful observation of the preparation always led to the conclusion that these were not within the tube itself, but belonged to cells above or below it. The state of things above indicated is best seen in radial longitudinal sections, which have become quite transparent by maceration for one or several days in very dilute solution of potash, without very considerable swelling of the cell-membranes, and which are thick enough to allow of following the tubes for a considerable distance. Accordingly I can only explain the septa, which Dippel represents as present in the young ends of milk tubes, as walls outside the tubes, or perhaps also as the contiguous walls of two tubes cut obliquely. The septa described by him as occurring here and there, I also have certainly been able to find not uncommonly at the nodes (but only there), in

Euphorbia Lathyris: they are thick transverse cellulose plates in the main tubes. They perhaps show, as above stated, that new branches and continuations of the tubes coming from below arise from cells of the meristem, which coalesce with them. Perhaps they are subsequently formed structures in the originally continuous sac.

Observations on the growing plant, from the stage of germination onwards, having constantly proved the existence of tubes which extend continuously into the extreme meristem, there was reason for supposing that these arise in the embryo in small number only, and that, once formed, they grow on with the plant in such a way that the whole system of tubes of the stock, exclusive of the layers of secondary cortex, is derived from their elongation and branching. In order to test this supposition, Herr J. Schmalhausen undertook in the laboratory at Strassburg an investigation of the development of tissues in the embryo of species of Euphorbia (E. Lathyris, Myrsinites, Lagascæ). I append the summary of his results up to the present time word for word, as it was given to me, with the remark that what is said on the coalescence of branches has, as above indicated, always appeared doubtful to me.

'The first initials of the laticiferous tubes appear at a very early stage of development of the embryo of Euphorbia. At that moment, when the cotyledons begin to make themselves prominent, there are single cells, lying approximately in the same transverse section of the embryo, which first distinguish themselves from those surrounding them by a peculiar refractive property of the cell-walls, which gives them the appearance of being swollen. At this time the plerome cylinder is clearly marked off at the apex of the root from the three-layered mantle of periblem and dermatogen by a boundary line, which appears sharply in optical section; while in the upper cotyledonary portion of the embryo no arrangement in layers is visible. Where the limit between the plerome cylinder and cortex of the end of the root ceases at the upper end of the latter, that is in the part belonging to the cotyledonary octants, the cells in question may be seen so placed that the line separating the plerome cylinder from the cortex leads up to the base of these cells. These original cells of the laticiferous tubes extend greatly at first in different directions, so that they can now be easily recognised by their great size. As the embryo continues to grow the cells increase in length, and, thrusting their upper and lower ends between the cells of the surrounding tissue, they put out processes upwards into the cotyledons, and downwards into the end of the root. Besides this, lateral processes are formed, which compose a felt in the node of the embryo, and surround its growing-point. Thus the sacs of the embryo are formed, not by coalescence of cells, but by apical growth of the processes of the original cells, which force themselves between the cells of the embryo: where two processes meet with their ends, the wall separating them is often absorbed, and a coalescence of the sacs takes place, as is the case also in the nodes and between the branches of the main tubes in young leaves (or cotyledons): this occasionally occurs also in the apex of the root.

'The best proof that the sacs have an independent apical growth, and do not arise by coalescence of cells, is obtained at the apex of the root, where they have a direct course. The processes of the original cells, which grow into the apex of the root, are arranged approximately in two concentric layers: one series of them belongs to the plerome cylinder—they permeate a layer of cells of the apex of the root, which is subsequently found to be within the layer of endodermis; the others

are found in the 2nd or 3rd layer of cells beneath the surface. Both series have an almost straight course, and not unfrequently they may be followed through their whole length from the node of the embryo to the apex of the root. Before reaching this, they terminate with diminished diameter, measuring hardly half that of the surrounding cells. Behind the tapering end the lateral walls are bulged out, with teeth, which fit between the surrounding cells: further back the diameter of the sac increases, the teeth are smoothed down, and their walls are only slightly sinuous: at the top, where the diameter of the sac is not less than that of the surrounding cells, or even greater, its walls are smooth. The appearance of such a sac gives the impression as though it were only with difficulty that it could find room between the cells to push in its apex, and that it endeavours, by extension, to fill up all possible cavities. The surrounding cells may at this time have firmer walls, while those of the tube are soft—therefore the young milk-tubes cling to the surrounding cells, and push out teeth between them. Later the walls of the tubes may become firmer, the inequalities smooth themselves out, and as the other tissues gain more space, the walls become quite even. Growing in this manner the tubes permeate the ripening embryo to the extreme apex of the root, and reach the seat of its future growth, viz. the limit between the apex of the root and root-cap.

'In the germinating seed other remarkable phenomena become apparent. While the apices of the laticiferous tubes grew up to this point between the cells of a slowly dividing, and slowly growing tissue, they are now surrounded by a quickly growing tissue, in the focus of growth of the apex of the root. Accordingly they enlarge here to the diameter of the surrounding cells, and even exceed them sometimes, and terminate with bluntly rounded ends, which often appear swollen, at the limit between the root-apex and the root-cap. The ends of the tubes are easily recognised by means of their dense contents; their blunt ends—like plastic masses—are easily found, and clearly marked. But there are never seen even traces of septa in course of solution, which would certainly be found here, if the tubes were formed by the disappearance of the walls separating the cells from one another. From the examination of longitudinal sections through the apices of roots of seedlings, it must certainly be concluded that the laticiferous tubes of the root of Euphorbia have an independent apical growth, and grow on continuously at the apex with the other tissues of the root.

'At the apical point of the stem the behaviour of the milk-tubes is much more difficult to observe, since they here take a very irregular, crooked course, and therefore cannot be followed for long distances. Terminations of the tubes are sometimes to be found above the youngest leaves, but their connection with tubes lower down could never be proved[1]: in the nodes a felt of tubes is always formed, from which branches run up towards the apical cone. There is no evidence against the tubes having here a growth fundamentally similar to that in the apex of the root, and none to support the idea that new milk-cells are successively formed in the growing point, which would subsequently grow out to tubes.

'It appears as though all the tubes of the Euphorbia plant owe their origin to a process of branching of the original cells formed in the embryo.

[1] I was able to prove this repeatedly in E. splendens and trigona.—De Bary.

'In Asclepiadeæ and Apocyneæ (apparently also in Ficus) the same seems to be the case also in the apex of the root of the germinating seed. The tubes are much narrower and difficult to follow. In the apex of the root they are distributed throughout the cortex. My observations on them are in other respects still very incomplete.'

The origin of the above-mentioned milk-tubes in the secondary bast, which is formed from the cambium, in Ficus, Morus, Broussonetia, Maclura, and Nerium, is not explained by the above observations; and I am unable, either from published accounts, or from my own observations, to propound any well-founded view whether they arise as branches of those in the primary cortex, and make their way into the secondary bast, or whether they are successively formed anew from the cambium, and in that case are in no direct connection with the primary tubes. Maclura aurantiaca may be especially recommended for the further pursuit of this question.

However great the differences in development, above noticed, between the non-articulated and the articulated tubes, still the frequently abundant branching of single members of the latter, and perhaps the coalescence of branches of the former to form anastomoses in the nodes, constitute a transition between the extremes of both categories; and even without these, other common points of structure and distribution, and of functions as indicated by the latter, would certainly lead to uniting both as one sort of tissue.

Brief allusion has above been made, in accordance with the views of Dippel and Hanstein, to their near relations to the sieve-tubes: this subject will be returned to in Chap. XII. These relations are mainly physiological, and topographically-anatomical. The assertions as to close histological relations between milk- and sieve-tubes are, I believe, wrong, or at least exaggerated; for instance Vogl's assertion that both the resin-passages of the Convolvulaceæ, which do not belong to this category, and the true milk-tubes, e.g. in the Campanulaceæ, develope from sieve-tubes, or at least may do so. Such a development never occurs. Again, it is especially stated by Dippel, both that the septa in articulated tubes—e.g. in Chelidonium and Papaver—are perforated like sieve-plates; and also that the lateral walls (e.g. Papaver, Cichoraceæ, Carica) are often provided with sieve-plates, and that thus there are in these cases intermediate forms between sieve-tubes and articulated milk-tubes. I could never find this phenomenon, but rather only smooth, delicately outlined pits on the lateral walls, or wide, sometimes grouped perforations. Schmalhausen's investigations on this point also gave the same result. Further, Dippel's drawings of these structures show little similarity to true sieve-plates of dicotyledonous plants. The septa often resemble them, it is true, inasmuch as they are perforated by more than one pore; but the pores are coarse, wide, and irregular, and have none of the other characteristics of structure of sieve-plates (comp. Figs. 80, 81). On the contrary, the sharp difference of structure between the sieve- and milk-tubes is always particularly clear, where one would *a priori* the most expect to find intermediate forms, i.e. where both are closely side by side, as is the case in the secondary bast.

The view, so long held, as to the near morphological relations between milk-tubes and sclerenchymatous fibres—'bast-cells'—has been above refuted. It was excusable that Mirbel at the beginning of this century confused the two organs, and came in 1835 to the conclusion that all the sclerenchymatous fibres of the secondary

bast are 'latexifères[1].' But Schacht's joy at having got rid of the laticiferous vessels and recognising them as branched 'bast-cells,' which he has repeatedly expressed since 1851, was obviously based upon his failure to recognise the true, delicate milk-tubes in Hoya and herbaceous Euphorbias, a failure which had less excuse at his time; further upon the opinion that the latex of these plants was contained in the thick walled sclerenchymatous fibres, which are often branched, and upon cognate and further confusion of the latter with the well-distinguished thick-walled milk-tubes of Nerium and succulent Euphorbias.

Finally, it is undeniable that in the family of the Papaveraceæ, in the Aroideæ, and Musaceæ, there is a near relation between the milk-tubes and peculiar sacs containing colouring matters and tannin. In the first the milk-tubes are absent in the rhizome of Sanguinaria, in Glaucium, Macleya, and the sacs containing colouring matter appear in their place: the other above-named genera are without these, and have laticiferous tubes. All those Aroideæ and Musaceæ which have been examined have tannin-sacs, variously distributed; in certain forms there are also found milk-tubes extremely rich in tannin, in place of which in many Aroideæ there are only rows of tannin-sacs. (On this point compare also Chap. XII.) All these anatomical relations remain inexplicable, till we know better than at present the physiological significance of their different contents. Here we cannot do more than draw attention to them. The anatomical facts above mentioned suggest that under the name Milk-tubes there are at present united two sorts of structures, which do not correspond in function, namely, in the first place those of the Aroideæ and Musaceæ, containing more especially tannin; on the other those of other milky plants, which have little or no tannin, and which are closely related to the sieve-tubes.

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[1] Mirbel, Exposition de ma théorie, &c., Paris, 1809, p. 247, &c.—Idem, Ann. Sci. Nat. 2 sér. tom. III. p. 143.

CHAPTER VII.

APPENDIX. INTERCELLULAR SPACES.

Sect. 49. Between the elements of mature tissue there are often cavities, which are grouped under the term intercellular spaces.

These arise in two ways in the original masses of cells, which, at least when in the state of meristem, are always in uninterrupted connection. Firstly, by separation of *permanent* tissue-elements, as the result of their unequal surface-growth in different directions, the original common walls splitting, while the common limiting layer which was originally present is—perhaps always—dissolved. Secondly, by disorganisation, dissolving, or in many cases rupture of certain *transitory* cells, or groups of cells, which are surrounded by permanent tissues. We may call the first mode of origin *schizogenetic*, the second *lysigenetic*, and, if a special term must be adopted for the mechanical rupture, it may be called *rhexigenetic*.

According to the stage of development at which the formation of intercellular spaces takes place, one may, with Frank [1], distinguish as *protogenetic* those which are formed on the first differentiation of tissues, and as *hysterogenetic* those which appear subsequently in old mature tissues.

According to their contents intercellular spaces fall into two categories. The first are filled with bodies or mixtures of the same sort as the secretory sacs treated of in Chap. III, or the secretory cavities of the epidermis; they are nearly related to these anatomically and physiologically, and spaces of these two categories not unfrequently appear even to act as substitutes one for the other. They may be designated secretory intercellular spaces, or *intercellular secretory reservoirs*. In treating of them reference has often to be made to the other, not intercellular, secretory organs.

The others contain from the very first only *air*, or in rare cases water. They form together a special ventilating apparatus for the tissues. The stomata of the epidermis (p. 34) are a part of this apparatus; they are a special case of schizogenetic and protogenetic spaces, which usually contain air, but also water in the special cases mentioned.

The same intercellular spaces rarely take part in both functions. Thus in the parenchyma of Lysimachia Ephemerum, where the fixed, red, resinous secretion, to be more accurately described below, partly covers the wall of the cells bordering on the

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[1] Beitr. zur Pflanzenphysiologie, p. 101.

air space, in some places as a thin layer, in others as thick masses filling the cavity, while again in other places it is entirely absent.

The intercellular spaces will be here more exactly treated, following the two main categories as defined by the character of their contents.

INTERCELLULAR SECRETORY RESERVOIRS.

Sect. 50. Hysterogenetic reservoirs of this category arise in old masses of tissue of long-lived plants from subsequent metamorphosis. Therefore, in order to avoid repetition, their treatment may be passed over for the present, and be resumed in Chaps. XIV and XV. We shall then speak here of *protogenetic* forms only[1].

These may be distinguished by their contents, and be named as those which contain *resin* and *ethereal oil*, or mixtures of both, or *Balsam;* further as containing *mixtures of gum*, or *mucilage*, or *gum-resin*.

According to form on the one hand there may be distinguished elongated, tubular *canals* or *passages*, permeating the tissues for long distances, and having a rounded or angular transverse section; and short, circumscribed, round or rather long, completely closed *hollows* or *cavities*, the latter being also indicated by the word of many meanings, viz. *glands* (comp. p. 92), and being further distinguished as internal glands, to avoid confusion with the outer glands belonging to the epidermis.

Between the general quality of the secretion and the form of the reservoir there is no generally constant relation; there are passages with balsam or mucilage, and cavities with the same contents, &c. On the other hand, in both cases there is as a rule a very constant, similar character of the reservoirs, according to the families, genera, or species in which they occur, so that they give to these very constant anatomical characters. The Coniferæ are a striking exception owing to the variety of form of their resin-reservoirs in the different genera. Unimportant exceptions occur here and there in other families: among the Compositæ, e. g. Tagetes patula has short closed sacs in the leaves, instead of the passages which are found in the other parts of this plant, and in the leaves of allied species. The same holds for the leaf of Mammea americana, in contradistinction to the other parts of this tree, and the leaves of other Clusiaceæ. Some further cases of this sort will be mentioned in the subsequent special descriptions, p. 206.

As already indicated, the reservoirs in question occur only in certain classes, families, and genera, and especially in those which have no other places for the production and storing of those secretions. A comparison of the statements in Chaps. I and III will make this clear, and will also call to mind the absence of any special secretory organs in the vegetative body of many plants. We may also shortly mention the mutual substitution and relation of the reservoirs in question with the milk-tubes in different genera and species, e. g. in the Compositæ and Aroideæ: this has been above indicated, and will be again treated in Chap. XII.

In rare cases a mutual substitution is found to take place between sacs and cavities with the same secretion, in different parts of the same plant. This also occurs

[1] Compare Frank, *l. c.*—N. Müller, in Pringsheim's Jahrb. V. p. 387.—Van Tieghem, Ann. Sci. Nat. 5 sér. tom. XVI.—[Also Szyszyłowicz, Sekret-behälter d. flüchtigen Oele. *Ref.* Bot. Centralbl. 1881, Bd. 8. p. 259.]

most prominently in Myrsine africana, and many species of Lysimachia, where the characteristic red resinous secretion occurs in sacs in the root, and in roundish intercellular cavities in the other parts of the plant.

The reservoirs in question may be arranged, according to their form and the nature of the secretion, in the following systematic groups.

1. *Mucilage- and gum-passages* in the *Marattiaceæ*, many *Lycopodia*, the *Cycads*, species of *Canna*, and *Opuntia*, and some *Araliaceæ*. Mucilage-containing cavities of lysigenetic origin occur in single cases, mentioned above among sacs (p. 144).

2. *Resin, ethereal oil*, emulsions of *gum-resin* of different quality, according to the special case, and often little known as regards chemical relations, occur—

(*a*) in *passages* in the *Coniferæ*, *Alismaceæ*, and *Aroideæ*, the *tubifloral Compositæ*, *Umbelliferæ*, *Araliaceæ*, *Pittosporeæ*, many species of *Mamillaria*, *Clusiaceæ*, *Anacardiaceæ*, the genera *Ailantus*, and *Brucea* of the family Simarubeæ.

(*b*) In *short cavities* in the group *Rutaceæ*, in the sense of Bentham and Hooker (exclusive of Simarubeæ and Zygophylleæ), in species of *Hypericum*, many species of *Oxalis*, *Myrtaceæ*, *Myoporeæ*, species of *Lysimachia*, *Ardisia*, and *Myrsine*: perhaps also in Gossypium.

The *wall* of all secretory spaces, which is made up of that of the neighbouring cells, is, with the exception of the above-mentioned special case of Lysimachia Ephemerum, always completely closed, the lateral walls of the cells, i. e. those perpendicular to the surface of the space, being joined together without interspaces. When, as is the case in the petiole of Marattiaceæ and Cycadeæ, the original cells, which limit a passage, are separated laterally from one another by continued growth of the surrounding tissue in a peripheral direction, the enclosure is completed by the next outer layer of parenchyma. The number of cells limiting the transverse section of a cavity varies according to the particular case. The small resin-passages, which run transversely between the larger longitudinal ones in the secondary cortex of Cussonia, are, according to N. Müller, at first at least, slit-like spaces between the partly separated walls of two rows of cells, and are thus limited in transverse sections by two cells. Most of these spaces appear in transverse section to be limited by 3, 4, or many more cells, the number of which may increase as the space widens by divisions placed radially with regard to the space. Fig. 85.

The cells surrounding the secretory reservoir have generally the properties of parenchymatous cells. In form they either do not differ, or only slightly, from the cells of the neighbouring parenchyma, e. g. in the young roots of the Compositæ, in the leaves of Ardisia crenulata: or, as in most cases, they are sharply distinguished, so that one might speak of a peculiar lining of the wall, or *epithelium* of the intercellular space. According as the peculiar character extends to one or several layers of cells surrounding the space, there may be distinguished one-, two-, or several-layered epithelium. The enclosure of the several-layered epithelium of the resin-passages in the leaves of Pinus Strobus, sylvestris, Laricio, &c., and of the roots of Philodendron, in a completely closed sheath of sclerenchymatous fibres, which are wanting in the homologous passages of other closely allied plants, is worthy of notice. The cells of the epithelium are generally prismatic in elongated passages; their greatest diameter usually lies in the direction of the length of the passage, only in the leaves of Cycads (Kraus, *l. c.*) do they lie transversely. Their transverse diameter is usually much

smaller than that of the neighbouring parenchyma, so that they appear very different from it in transverse sections: in rare cases they are distinguished from it by their greater width (roots of Compositæ, branches of many species of Rhus according to Trécul). Their inner surface is often slightly convex towards the passage; in the mucilage-passages of the Marattiaceæ it is even elongated and conical: in those of the leaves of Lycopodium the cells bulge in a club-like manner. Where an epithelium can be distinguished in isodiametric cavities (Lysimachia punctata, and its ally, Myrsine) the cells are flattened towards the surface of the cavities.

The wall of the epithelial cells is delicate, in resin- and balsam-passages often coloured brown or yellow. In the mucilage-passages of old leaves of Cycas revoluta alone it is stated by Trécul[1] that they are strongly thickened on the side next the passage.

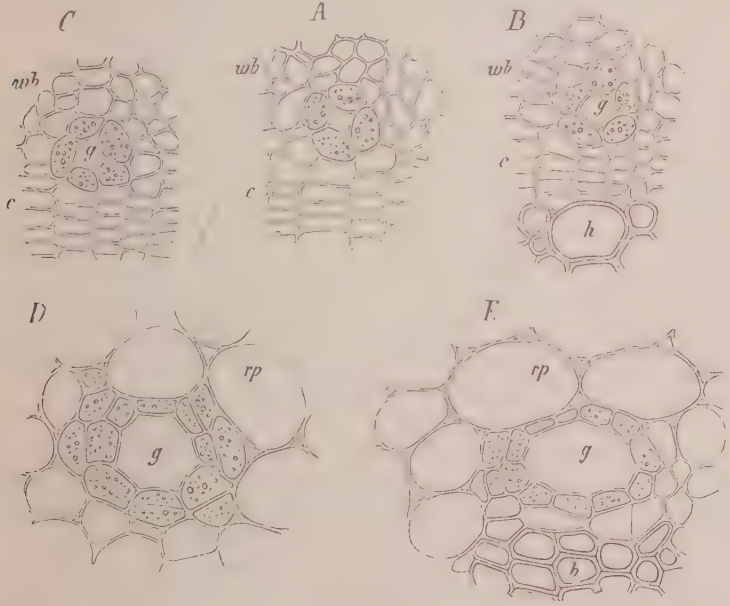

FIG. 85.—Hedera Helix; transverse sections of the young stem (800); *g* resin-passages. These are in *A*, *B*, *C* young, and have appeared between four and five rows of cells, in the secondary cortex *w b*, at the limit of the zone of thickening *c*; *h* wood; in *D* and *E* older, larger passages; *b* bast; *r p* parenchyma of the outer cortex. From Sachs' Textbook.

There is a great lack of investigations on the protoplasm and contents of the cells of the epithelium, and of the surroundings of the secretory reservoirs generally. It seems to be certain for all cases that they contain small masses of the secretion, which then filter in some way in mass through the membrane into the reservoir. The cells surrounding the young oil passages in the roots of Compositæ have clear contents, in which, in Helianthus annuus[2], large quantities of tannin are shown to be present by reagents; this is also the case with the oil in the passages. In Tagetes patula[3], at the transition from the root to the hypocotyledonary stem, a clear violet

[1] L'Institut, 1862, p. 315.

[2] Sachs, Botan. Zeitg. 1859, p. 183.

[3] Van Tieghem, *l. c.* p. 113.

cell-sap makes its appearance in the cells bordering on the passages: further up and throughout the stem orange-yellow granules, which turn blue with iodine, are also found fixed upon the wall of the cells next the passage. In the limiting cells of young passages of the secondary cortex of Pittosporum Tobira, Müller mentions numerous starch grains with a covering of yellow oil. The epithelial cells of the reservoirs in the leaf of Ginkgo, in the stems of many Compositæ, e. g. Solidago lævigata, contain chlorophyll grains: those which surround the round resin-reservoirs in the leaf of Ardisia crenulata are, with exception of the necessary peculiarities of form, in no way different from those of the rest of the chlorophyll parenchyma, to which they belong.

In many plants which secrete resin (Coniferæ, Anacardiaceæ, Umbelliferæ, Araliaceæ, Compositæ) Müller has by staining with Alkanna found drops of resin not only in the cells bordering on the reservoirs, but distributed widely in the surrounding tissues. Without wishing in the least to combat the correctness of these observations, I regard further careful investigation of the contents of these cells as the more desirable, since very thin sections, which Müller states that he used almost exclusively, are not the most suitable preparations for the study of protoplasm and cell contents.

The contents of the intercellular secretory reservoirs form in most cases a homogeneous fluid mass, or an emulsion-like mixture without characteristic peculiarities of structure. Their chemical properties are indicated approximately, and for the present sufficiently, by the names above used. The red secretion in the cavities of species of Lysimachia and Myrsineæ, which, from its solubility in alcohol, may, till further investigated, be classed with the resins, is an exception to this rule, since it appears in a fixed form, and with apparently crystalline structure, as will be described below. The same seems to be the case, judging from incomplete investigation, in many species of Oxalis.

The large mucilage-passages, $\frac{1}{2}^{mm}$ wide, of the Opuntias are characterised by containing numerous and large crystals of calcium oxalate embedded in mucilage. As regards the material characters of the milky contents of the passages of Mamillaria angularis, and its allies, which will be more accurately described below, I have come to no certain conclusion.

The *mode of development* of the intercellular secretory reservoirs is for the *lysigenetic* forms generally as follows: that, in a group of delicate cells, which arise by definite meristematic divisions, and which correspond in form and arrangement to the future reservoir, the secretion appears at the expense of the original protoplasmic body, and that subsequently the walls of the cells are dissolved, and the separate secretory masses coalesce. Of reservoirs of this category, containing gum and mucilage, only the passages of the periphery of the petiole of the Marattiaceæ have as yet been carefully investigated, and in their case it is shown, that the elements of the simple row of cells corresponding to the subsequent cavity of the passage are filled with the secretion before they are broken up. Nothing is known of the form in which they first appear. In the investigated reservoirs of ethereal oil and resin the secretion first appears as small drops in the protoplasm of the cells about to be broken down. These increase quickly in size and number, and coalesce after the disappearance of the walls, to larger masses. Where the original cellular body consists of several

layers, the process of breaking down and of coalescence progresses centrifugally (comp. Fig. 86, and above, p. 69, Fig. 22).

This mode of development holds for the gum-passages in the *periphery* of the petiole of the Marattiaceæ, for the mucilage-passages of the Opuntias, which require further investigation, and perhaps also of the Mamillarias; again for all secretory cavities investigated, with the exception of those of the Lysimachias, Myrsineæ, and species of Oxalis. Doubtful cases will be named below.

The *schizogenetic* spaces (comp. Fig. 85, p. 203) appear sometimes between cells, which resemble those surrounding cells which do not border on secretory reservoirs, both in arrangement and origin: sometimes they are produced by peculiar divisions of special initial meristem-cells. The first case is found to occur in the above-mentioned spaces of Lysimachia Ephemerum, and in the slit-like transverse passages of Cussonia also noted above. Further, the large longitudinal passages in the secondary cortex of the same plant and of other ligneous plants arise between the common corners of junction of four rows of cells, which are produced from the cambium in the same way (Chap. XIV) as its other products. The same holds, with many special modifications it is true, for the formation of the resin-passages in the secondary wood of the Abietineæ[1]. The prismatic longitudinal passages at the inner limit of the primary cortex in the roots of Compositæ are, excepting in the appearance of the characteristic contents, formed in the simplest and most common case, in the same way as those air-containing cavities found in the external layers of the cortical parenchyma, viz. at the corners of contact of four rows of cells.

On the other hand, the primary passages in the pericambium of the roots of the Umbelliferæ, which will be described later (Chap. XIII), are the result of special meristematic divisions. The passages in the primary cortex of the Abietineæ, and in the leaves of Cycas and Alisma, may each be traced back, according to Frank and N. Müller, to a row of initial cells, which divide longitudinally by successive crossed walls: the four daughter cells then separate at the angle of contact to form the passage.

As the plant grows there occurs, as has been shortly noted above, a widening of the passage, and growth of the cells which enclose it, in a direction tangential to its surface: this is accompanied by increase in number of these cells by radial division, e.g. from the four original cells to 6 or 8 in Pinus and Alisma (Frank); in cases of long-continued growth in thickness of the part, and correspondingly great widening of the passages, the number may reach much higher figures, e.g. cortex of Coniferæ, Rhus, Pittosporum, &c. On the other hand the cells surrounding the space may also divide in a tangential direction, and the originally single limiting or epithelial layer may be doubled, or divided into several layers, e.g. in the passages of species of Philodendron, the cortex of Pittosporum, Hedera (Fig. 85), and the leaves of Pinus. This mode of origin of several layers of epithelium from the originally simple limiting layer is not proved for all cases where they occur, and another origin is in many cases quite possible for the outer layers.

The origin of the secretion contained in the schizogenetic spaces, looking at it from the purely histological side, and neglecting the chemical questions, is in my opinion not clear, and requires further investigation. It is obvious that it, or at least

[1] Sanio, in Pringsheim's Jahrb. IX. p. 99.

the material for its formation, must be derived from the cells, which closely or immediately surround the space. Where it is possible, as e. g. in the case of the above-mentioned resinous secretion around the reservoirs, to prove its presence in the cell-contents, it may be assumed that it passes as such from the cells into the reservoirs, of course not by filtration in great masses, but, as Müller assumes, by diffusion through the membranes in successive small quantities. This view is supported by the fact that, according to Müller in the Coniferæ, and Sachs and van Tieghem in the roots of Compositæ, the intercellular spaces are first present without the characteristic secretion, and that this first appears in them at a later stage.

On the other hand there occur, as above stated, cases where the secretion is also of a resinous nature, but is not proved to occur as such in the cell-contents in the vicinity of the reservoir. Further, Sanio has recently expressly stated that the resin-passages of Pinus are filled with the secretion even from the time of their first origin [1]. So far as my investigations extend, the young stage of the passages of the root of Compositæ, when the secretion is absent, is at best very transitory: the secretion appears very early, and may be easily overlooked in the narrow young passages: it may be really absent, especially in transverse sections, since it may have flowed out.

Since, in the dermal glands of the epidermis, secretions, which are in every respect similar to those under consideration, are often to be first observed anatomically as constituents of the cell-wall, and further since the intra-mural glands (p. 96), when regarded purely histologically, are merely a special case of schizogenetic secretory cavities in the epidermis, the question arises, whether in all cases the secretions of schizogenetic reservoirs are not to be regarded as constituents of the cell-wall. The actual observations supporting this view are of at least equal weight to those supporting the other, while none of the latter exclude the correctness of the former view.

All secretory *passages*, with the exception of the few named on p. 205, are of schizogenetic origin; of these however the mucilage-containing passages in Canna must be more exactly investigated; also besides those cavities already mentioned in Lysimachia, Myrsineæ, and Oxalis, those which take the place of passages in many short leaves of Conifers deserve further attention.

Further descriptions in detail of the secretory *passages* must so often have reference to their arrangement, that, to avoid repetition, they must be given subsequently in Chap. XIII.

Here those which are found in species of Mamillaria will alone be described. In the literature I find it only briefly mentioned that these plants have latex (De Candolle), which is contained in passages (Unger). Investigation shows, firstly, that the Mamillarias are entirely without those mucilage-sacs (p. 143) which occur in the allied genera. I also find no trace of intercellular secretory reservoirs in small species, as M. glochidiata and the like, and in an unnamed, very robust species. On the contrary, M. angularis, Hystrix, and Zuccariniana have a complex system of branched passages. These are limited, as seen in transverse section, by one 4–5 celled layer, or by two, or even three concentric layers of delicate cells, flattened tangentially to the passage: the width of the passages is about equal to that of one large cell of the parenchyma. They contain a thick, uniformly finely-granular, colourless juice, which emerges on section in large white drops, and hardens

[1] *l. c.* p. 101.

quickly in the air without change of colour. This must be a peculiar mixture: water, alcohol, ether, benzine, and alkalies do not alter it on the whole, though each reagent may dissolve a small quantity of it. When burnt it leaves behind a very small residue of ash. I have not obtained a clear idea of the mode of origin of the passages of the Mamillarias.

The crystal-containing passages of the Opuntias, which may attain a width of $\frac{1}{2}$ mm, are apparently of lysigenetic origin; in the mass of mucilage the cells, from the disorganisation of which they arise, are still partially recognisable.

Some details concerning the secretory cavities remain to be added, and statements may also be looked for regarding their occurrence and arrangement.

(*a*) The **Myrtaceæ**, judging from observations on numerous species of Eucalyptus, Melaleuca, Callistemon, Eugenia, and Myrtus, are generally provided with *oil-cavities*. In horizontal leaves these are particularly numerous on the upper surface, though not confined to it, and their epithelial layer is contiguous with the epidermis, in which those cells which touch the epithelium differ from the rest in form and size. In Myrtus communis, for instance, two semicircular epidermal cells are contiguous with the wall of the cavity at the upper side of the leaf: these cells are distinguished from the rest by their lateral walls not being undulated, and by their being only half as high. In the outer cortex of the branches, according to investigations on species of Eucalyptus, they are separated by some few layers of parenchyma from the epidermis. They have an approximately spherical form: the larger ones may be seen with the naked eye as transparent points, others are smaller, *e.g.* in the leaves of Eugenia australis. The cavity, which is filled with mixtures of oil and resin, is limited by a continuous epithelial layer composed of tabular cells. According to Frank[1] the cavities in the leaf of Myrtus communis are of schizogenetic origin. A round, thin-walled cell, lying beneath the epidermis, divides successively into 8 octants; these separate at their central point of contact, so as to form directly an intercellular space filled with oil, and this gradually assumes the form of the spherical cavity; the original eight epithelial cells meanwhile stretching tangentially, becoming flattened, and occasionally dividing. This description is contradicted by Martinet's short statement, according to which the oil-cavities of the Myrtaceæ arise like those of Citrus in a lysigenetic manner, a view which, though I have not observed their development myself, I must consider to be correct, from the agreement of the mature cavities with those of the Rutaceæ.

(*b*) The presence of *oil-cavities* is a general and characteristic phenomenon in the members of the group **Rutaceæ** in the sense of Bentham and Hooker, *i.e.* the families or divisions of the Rutaceæ, Diosmeæ, Boronieæ, Zanthoxyleæ, Flindersieæ, Toddalieæ (Skimmia), Aurantiaceæ, Amyrideæ[2]. The Simarubeæ and Zygophylleæ are excluded from this group, and have no oil-cavities.

The distribution of the organs in question, and their relation to parenchyma and epidermis, is, as far as investigated, the same as that in the Myrtaceæ. In the stem of Dictamnus and Correa alba they lie directly under the epidermis, in the leaves of species of Agathosma and Diosma especially or exclusively on the under side of the leaf—relations which are found also in the Myrtaceæ. They also correspond to these in average form and size. Their origin is in all cases lysigenetic. Even Frank's drawing for Ptelea trifoliata does not contradict this, though according to his description of the process of development their origin is schizogenetic. Rauter[3] gives a very exact history of development of the oil-cavities on the upper surface of the leaf of Dictamnus (Fig. 86). A cavity (*A*) originates from two cells, one an epidermal cell, the other a cell of the hypodermal parenchyma. The first divides successively into four cells, placed crosswise

[1] Beitr. p. 125.

[2] Compare Engler, *l.c.* on Amyris; also Van Tieghem, *l.c.* p. 173.

[3] Trichomgebilde, &c. *l.c.* p. 21.

in the epidermal layer; each of these is again divided into an inner cell next the parenchyma, and a superficial cell (*d*, *c*). The superficial cells increase further so as to form the portion of the epidermis which covers the cavity (*B*, *c*, *d*). The inner ones take a direct part in the formation of the cavities. The chief part of the cavity originates it is true from the products of division of the primary parenchymatous cell (*A*, *p*, *p*), which divides by alternate horizontal and vertical divisions into numerous daughter cells; these, together with the similarly formed products of division of the inner epidermal cell, form a compact round body of numerous small cells. In the protoplasm of all cells of this body, which are at first very granular, there appear, after the division and growth have ended, more and more numerous drops of ethereal oil; then the delicate membranes are dissolved, and the oil drops coalesce to large drops (*o* in *C*). The process begins in the middle of the body, and proceeds centrifugally to its surface. The oil-containing cavity thus formed is limited, with the exception of the epidermis, by cells of the surrounding parenchyma, which are more or less flattened towards the surface of the cavity; these cells, being in uninterrupted contact with one another, completely enclose the latter. The cavity in the hairy dermal warts of the Dittany arises, as described p. 69, in the same way.

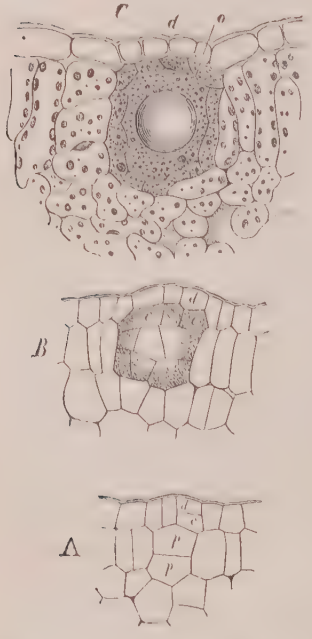

FIG. 86.—Dictamnus Fraxinella; oil-reservoirs of the upper side of the leaf; transverse section; *C* (200) mature; *A* and *B* successive young stages of development (320). Further description in text. After Rauter from Sachs' Textbook.

The oil-cavities of Ruta have in the main the same development. That of Citrus differs at most in small secondary peculiarities, which need not be described in detail here. Martinet, who described them, has traced their origin back to a condition in which the transverse section shows three small cells in the epidermal layer, with abundant protoplasm, and beneath these three inner cells. The arrangement of these cells is such, in these youngest cells and in rather later stages (*l. c.*, Fig. 234 and 235), that it is probable that their mode of origin is the same as that described by Rauter for Dictamnus. It can hardly be doubted, after investigation of mature or half-formed stages, that those of the other members of the group of Rutaceæ have fundamentally the same origin.

The cavity is always completely and smoothly isolated by the close connection of the cells of the surrounding tissue, so that in good sections it may be taken for a single large cell lying between these. As is especially evident in the chlorophyll-containing parenchyma, the cells of the limiting layer do not differ fundamentally in structure from those of the mass of tissue, in which the cavity lies. Obvious remnants of partially dissolved delicate cell-membranes are not unfrequently to be found; these form a more or less irregular covering to the wall. It is possible that in many cases the mass of delicate cells, instead of being dissolved, persists in whole or in part. Many figures of Engler appear to point to this. But here, even with tolerably good preparations, it is possible to be deceived, since the sections often do not cut the cavity in a median plane, but lay bare portions of their wall, which then appear in surface-view as dense, multicellular bodies.

(*c*) The spots, recognisable with the naked eye as transparent points, in the lamina of **Hypericum** perforatum, and its allies, are oil-cavities of flattened spherical form, which occupy almost the whole space between the portions of epidermis of both leaf-surfaces which cover them, and are separated from the lower epidermis by at most one layer of parenchyma. Their structure, or that of the tissue surrounding them, is fundamentally

that described for the group of the Rutaceæ. Their origin, judging from observations described, can hardly be other than that stated by Martinet, viz. lysigenetic, though Frank describes it as schizogenetic. Cavities of the same sort occur in the superficial parenchyma of the cortex of the stem. In those of the stem of Hypericum balearicum Unger [1] found papillose and hair-like processes rising from the wall into the cavities. Many species of Hypericum, e.g. H. calycinum, canariense, hircinum, &c., have no transparent spots recognisable with the naked eye: it is uncertain whether the oil-cavities are absent in these cases, or, more probably, are only smaller than in the punctate species, or are in some way hidden.

(*d*) The bodies scattered in the parenchyma of species of Hypericum, which contain violet colouring matter, and are described by the above authors as glands, may here be mentioned, and recommended for further research: also the similar bodies in **Gossypium**. In the leaves of some species of Hypericum, these consist of spherical, loose aggregates of round cells; the colouring matter apparently lies between them. In the leaves of Gossypium they are round, undoubtedly lysigenetic cavities, which are filled with the violet colouring matter, soluble with difficulty in alcohol.

(*e*) Among the **Myoporeæ** the species of Myoporum have numerous round oil-cavities of unequal size in the leaves and the outer cortex of the branches. The cavities are superficial, and separated only by one or two layers of cells from the epidermis, which is arched convexly outwards, e. g. M. parvifolium: in M. tuberculatum, on the contrary, according to Unger [1], they occur in the middle of the chlorophyll-parenchyma of the leaf. They are surrounded by 1–3 layers of flattened cells. As far as investigated, their origin appears to be lysigenetic.

(*f*) In the parenchyma of species of **Lysimachia**, of **Myrsine** africana, and **Ardisia** crenulata a resinous body is found in intercellular spaces; it is soluble with difficulty in alcohol, easily soluble in ether, of a bright brownish red colour, and forms fixed, often almost brittle masses: its chemical properties require closer investigation. Its mode of distribution differs in special cases, and of those plants investigated it is simplest in Lysimachia Ephemerum. In the root of this plant it appears in most of the usual prismatic, air-containing, intercellular spaces as a finely granular covering on the wall of the adjoining cells: here and there it is interrupted, while in thickness it varies from that of an insignificant layer to such a bulk as to fill up the passage. In the very lacunar parenchyma of the pith and cortex of the stem, it has fundamentally the same distribution, but is less regular, owing to the irregular form of the cavities: in neighbouring cavities it is contained in very unequal quantities, in many not at all. When secreted in quantity, it forms on the cell-wall a convex covering, striated perpendicular to its surface. Finally, it is found in the leaves, in the cavities of the chlorophyll-parenchyma, as thick, irregularly shaped masses, with indistinct radial striation: the cavities are surrounded sometimes by ordinary cells, sometimes by a more or less distinct layer of flattened cells.

The secretion is strongly localised in the leaves and the cortex of Lysimachia punctata [2] and of Myrsine, in the leaf of Ardisia, and of most Lysimachias. Here round reservoirs, which appear as points to the naked eye, are found in the parenchyma: they are surrounded by about eight flat, closely connected, chlorophyll-containing cells, and filled with the dense red secretory body, which is in Myrsine radially striated in a remarkable way. The reservoirs arise schizogenetically, and contain the secretion as soon as they are visible. In the cortex of branches of the above Ardisia, the reservoirs are rarely round, usually elongated, spindle-shaped, appearing as little strokes more than 1^{mm} in length.

In the roots of Lysimachia vulgaris and punctata, and of Myrsine, the secretion does not lie in intercellular spaces, but in single sacs or cells, not distinguished in size or form from the surrounding cells of the parenchyma: in each of these there is a body of the

[1] Anatomie und Physiologie, p. 213.

[2] P. Moldenhawer, Beitr. p. 162.—Meyen, Secretionsorgane, p. 61.

same structure as that in the reservoirs of the leaf, which does not completely fill the cavity, being surrounded, while young, by colourless granular contents (protoplasm?). In the roots of Ardisia I did not find the red secretion.

(*g*) Many, though not by any means all the species of **Oxalis** from the Cape and America have, on the under surface of the leaf, and running towards the margin, rather prominent reddish bands, which are mentioned in descriptions as glands or wales. In the species—not exactly defined—which I have investigated, these bands are reservoirs quite similar in the colour, consistency, and radiate structure of the secretory mass, and also in the structure of the surrounding tissue to those of Lysimachia punctata and Ardisia. They lie in the chlorophyll-parenchyma, and are separated by but one layer of its cells from the distended epidermis of the under surface of the leaf. Thorough investigations were not made [1].

INTERCELLULAR SPACES CONTAINING AIR AND WATER.

Sect. 51. Air- and water-containing intercellular spaces occur, on the one hand, in many *vascular bundles*, and these will be treated of in Chap. VIII; on the other hand, they are a characteristic component of large masses of thin-walled assimilating *Parenchyma*. Intercellular spaces are absent only when the parenchyma forms definite sheaths.

The cavities in question extend between all cells, so that each one of the latter borders on one or several. They together form, as will be again mentioned below, a continuous system throughout the plant, which opens into the stomata, where these are present. The spaces sometimes contain water in the vicinity of the water-pores, elsewhere they normally contain *air*, i. e. a mixture of gases similar to atmospheric air, in which the proportion of oxygen and carbonic acid varies with the activity of the processes of assimilation and respiration [2].

The whole volume of the air-spaces varies greatly in special cases, and is often very large in proportion to the volume of the part of the plant which is not filled with air. Approximate measurements, which Unger [3] made on leaves and petioles of 41 species of plants, gave as minimum 77 parts by volume of air to 1000 parts of the leaf in Camphora officinalis, and as maximum 713 to 1000 in Pistia texensis. The air of the vessels and that diffused in the cell-sap, which would be also pumped out, is not taken into account in these statements: but it appears that this is on the whole of minor importance, and that on the other hand the figures obtained would be sometimes lower, sometimes much higher, if the single masses of parenchyma composing the leaf were investigated separately.

It was long ago known that the whole volume of the air-spaces in relation to that of the whole plant is largest in plants of all classes and families which grow in water, or in moist positions, and on the other hand in those which inhabit dry places, as many Compositæ, Umbelliferæ, Labiatæ, Grasses, &c. with hollow stems or petioles.

According to their gradual, and not distinctly limited differences of relative

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[1] [See further, Russow, über sekretführende Intercellular-gänge der Acanthaceen, &c., Dorpat. 1880.—Bot. Centralbl. 1881, Bd. 5. p. 365.]

[2] Compare Sachs, Experimentalphysiologie, p. 262.

[3] Beitr. z. Physiol. d. Pflanzen. I. Sitzgsbr. d. Wiener Acad. Bd. XII. p. 367.

width, the air-spaces may be divided into *Interstitial spaces*, such as are of smaller volume than the adjoining elements; *cavities*, *lacunæ*, of almost equal or slightly larger volume; *passages*, *chambers*, and *hollows* of much greater relative volume. The tissue permeated by air-spaces may accordingly be termed lacunar, chambered, &c., and that with only narrow interstitial spaces may be called (relatively) dense.

The air-spaces of dense and lacunar parenchyma always arise schizogenetically at the first commencement of differentiation of the tissues. In preparations seen by transmitted light they may be seen close behind the growing-point, by reason of the air contained in them, as black bands between the cells. Comp. e.g. in Fig. 3, p. 10, the regions marked *m* and *r*.

The *interstitial spaces* of *dense* tissue run as a rule between the rounded corners of the cells, which are closely connected over the greater part of their walls, as narrow angular canals, the number of their sides being equal to the number of cells which border on them. Thus, e.g. the numerous three-sided prismatic interstitial air-spaces in regular polyhedral cells arranged in alternating rows, the four-cornered ones between the cells arranged in radial and concentric rows which are not alternate, in the inner primary cortex of many roots (Fig. 51, p. 124). More rarely they form narrow slits, standing serially one above another, and separated one from another by connected portions of the walls, these slits lying between the limiting surfaces of two contiguous cells, as in the dense tissue of the leaf of Myrtaceæ, species of Scirpus, the parenchymatous lamellæ of the cortex of Pilularia and Marsilia: this condition is allied to that of the many-armed lacunar tissue.

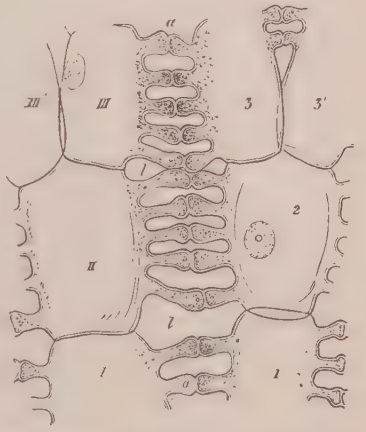

FIG. 87.—Sagittaria sagittæfolia; root, transverse section; *I—III* and *1—3*; two radial rows of many-armed cells from the cortical parenchyma; *a* arms; *l* cavities (350). From Sachs' Textbook.

Of *lacunar parenchyma* there may be distinguished two chief forms, which however cannot be sharply separated. The first (Fig. 87) arises through the unequal growth in surface of all cells as they pass from the meristematic state, in such a way that at certain points they put out processes which may grow to long arms, at other points these are not formed. The ends of the processes of adjoining cells remain connected with one another; between the other parts of the surface the intercellular space is formed. According as the processes are short, or are extended as long arms, and are arranged in one or several radial planes, the form of the cells and of the cavities varies. Almost all imaginable forms occur in the lacunar part of most bilateral leaves of all classes, with at the same time various transitions to lamellar parenchyma. Such parenchyma composed of 'stellate' cells occurs besides in many Monocotyledons, especially marsh- and water-plants. As examples of this are the diaphragms of air-passages, to be mentioned below: stellate bands (which will also be returned to below), alternating with the denser masses of parenchyma which contain the vascular bundles, traverse the petioles of the Marantaceæ longitudinally (species

of Canna, Maranta, Phrynium, Thalia), the leaves of many Bromeliaceæ, e.g. B. Caratas: cells, branched in a stellate manner in all directions, with long arms, and small central portion, form the inner part, the 'pith' of the halm of many species of Juncus: similar stellate cells, but with a large bladder-like central portion, compose the massive lacunar inner cortex of the Rhizome of Scirpus lacustris, Sparganium ramosum, &c.

In Dicotyledonous water-plants, stellate lacunar parenchyma is rare, with exception of the tissues of foliage leaves; still, according to Duval-Jouve, it composes the diaphragms of the air-passages of Limnanthemum nymphoides, and, according to Planchon[1] and Trécul[2], those of Nelumbium; also the spongy cortical mass of the roots of species of Jussiæa, and of the internodes of the stem of Mimoseæ, which serve these plants as floats.

The spongy air-containing cortex of the adventitious roots, which spring from the nodes, and which serve as floats for those branches of amphibious species of Jussiæa (J. repens, J. grandiflora, J. natans, J. helminthorrhiza) which grow in water[3], consists of 3–6 armed cells. They are arranged in concentric layers, and each puts out at least three narrow cylindrical arms from a not distended central portion. Of these the longest is horizontal and directed radially towards the periphery, and its end is connected with the opposite face of a cell of the next outer layer. The two shorter are in the simplest case radially and tangentially vertical, and of equal length, so that the radial view of the cell has the form of a procumbent ⊢. The end of each is connected with the corresponding one of the next upper or lower cell of the same layer. A connection of the cells of a layer in a tangential direction is finally brought about, sometimes by single tangential arms, sometimes by oblique direction of the halves of the cross-bar of the T. Radial and transverse sections thus show between the narrow arms very large, four-cornered air-cavities, which are continuous one with another. The length of the arms and of the air-cavities is nearly equal in each of the concentric layers, and increases successively from within outwards. The radial arms of the outermost layer abut directly on the epidermis, which soon breaks away and collapses. Also the spongy cortex of Desmanthus natans W., and apparently other similar Mimoseæ, may be here described, though from its mode of origin it should be ranged under secondary formations. The internodes of the stem of this plant, which grow horizontally in the water, are, according to Rosanoff[4], at first cylindrical; their parenchymatous outer cortex consists of an inner part, which is composed of 3–4 layers of roundish rather large parenchymatous cells, and an outer consisting of 3 small-celled layers covered by the epidermis. When the extension of the internode is ended, it swells to a shape like a barrel as the result of the appearance of the spongy floating apparatus. The formation of the latter begins with tangential divisions of the third layer of parenchyma from without, which, together with the changes which follow, are then continued successively in the more internal layers. The cells formed by the tangential divisions are arranged in radial rows, and grow to irregular stellate sacs with narrow cylindrical arms, while the central portion is not distended: the ends of the arms remain connected; the cells thus enclose wide lacunæ filled with air. Each second or third radial row is branched, and connected especially in the tangential direction, the 1 or 2 rows between them are branched on all sides. The epidermis and the hypodermal parenchyma are torn into narrow rags by the spongy swelling. Later the whole spongy apparatus is thrown off as bark.

[1] Flore des serres, tom. VI. [2] Ann. Sci. Nat. 4 sér. I. p. 168.

[3] Ch. Martius, Sur les racines aérifères des espèces aquatiques des Jussiæa, Mém. Acad. de Montpellier, tom. VI (1866).—Frank, Beitr. z. Pflanzenphysiologie, p. 152, fig. 24.

[4] Botan. Zeitg. 1871, p. 829, Taf. X.

If in the stellate lacunar tissue one arm of a cell be separated by a septum as a special cell from the central portion, as often happens, e. g. in Jussiæa, and if this cell divides further, the intercellular space is no longer limited on all sides by parts of branched cells, but, according to the number and direction of the successive divisions, by whole cells or by rows of cells, or simple or compound layers, or *lamellæ*. We may distinguish the more developed forms of this arrangement from the stellate tissue as *lamellar* porous parenchyma, though it is obvious that frequent intermediate forms prevent a general sharp distinction.

In the formation of lamellar parenchyma, unequal surface-growth and divisions of the cells which are passing from the meristematic stage keep pace with one another, at least at first, so that the width of the air-cavity and the number of cells which limit it laterally increase simultaneously: it is only in the last stage that the cavity is increased by extension of the cells alone[1]. It is not certainly proved whether the other case, which may be observed in the formation of many secretory reservoirs, and in the secondary cortex of Dicotyledons, viz. that the intercellular air-space appears after the divisions in its vicinity are ended, occurs also in the primary parenchyma.

Lamellar parenchyma occurs in certain plants in the same positions as stellate parenchyma in others; e. g. lacunar layer of the bifacial leaves of Ilex aquifolium, Arbutus Unedo, Eugenia australis, Camellia: base of the petiole of Aspidium filix mas and its allies: cortex of the rhizome of Carex disticha: stems of many Aroideæ, as Acorus Calamus, Calla, Monstercineæ, &c.: pith of Saurureæ.

As a special intermediate phenomenon between lamellar and stellate parenchyma may here be named the layer consisting of loose and irregularly connected rows of cells, which lies in the Selaginellas between the firm bundle sheath and the tough and dense surrounding tissue. (Comp. Fig. 131, Sect. 78.)

Wide air-containing *chambers* and *canals*, the diameter of which greatly exceeds that of the surrounding cells, are produced in two ways. Those of the one category arise schizogenetically, and are only distinguished from the lacunæ of lamellar parenchyma by their width. The others are formed lysigenetically, or better rhexigenetically: during their development a mass of tissue lying in the direction of the subsequent cavity ceases to follow the surface-growth of that surrounding it, and, since growth continues in the latter, the former is ruptured and more or less destroyed.

To the first, schizogenetic, category belong the larger air-spaces in stem, roots, and leaves of many marsh and water-plants; Marsiliaceæ, Salviniaceæ, leaves of Isoetes, Ceratopteris; Potamogeton, Hydrocharideæ, Alismaceæ, Pontederia, Aroideæ, Lemna; Papyrus (?); Ceratophyllum, Myriophyllum, Hippuris, Trapa, Hottonia, Elatine, Utricularia, Menyantheæ, Nymphæaceæ, Nelumbium, pith of Desmanthus natans, &c. Comp. Figs. 88, 112, 122, and 124, Chap. VIII.

To the category of lysigenetic forms belong the air-passages of the Equiseta, those of the leaves, stems, and roots of most Cyperaceæ, and Gramina, the leaves of Sparganium, Typha, Iris pseudacorus, and its allies, Pandanus, the Marantaceæ, Musa (?); in part those of the stem of Callitriche, those of the leaves of the narrow-leaved Eryngia, of Lobelia Dortmanna, Nelumbium (?), &c.; lastly, the axile tubes of

[1] Compare, e. g. Frank, *l. c.*—Vöchting, Myriophyllum, N. acta Acad. Leop. vol. 36.

numerous hollow stems of Equisetum, Grasses, Umbelliferæ, Labiatæ, Compositæ, &c., of hollow leaves and petioles (Allium, Asphodelus, Umbelliferæ, &c.), also the axile cavity of the internodes of Nelumbium[1].

In many cases the origin of the chambers has not been carefully investigated, but it may be recognised with some certainty from the structure of their mature walls (which will be described below), in the same way as in the instances marked (?) above. More accurate detail on this subject has but slight interest. On the one hand the two modes of origin are fundamentally different in extreme cases, usually also certain differences in structure of the walls of the chambers are peculiar to each, and lastly they are distributed as a rule in different systematic groups. But on the other hand all sharp limits are here again obliterated by all sorts of intermediate cases, while forms differing in origin and structure may be substituted one for the other, in the same position, in closely allied plants. For instance, the peripheral air-passages which alternate with the vascular bundles in the stems of the Equiseta are of intermediate structure and origin: they originate schizogenetically; finally, some of the separating cells are broken up and their membranes remain attached to the wall of the passage[2]. The same holds for the large air-passages opposite the two shorter sides of the quadrangular transverse section of the stem of the Eucallitrichæ, while the smaller ones there and in Pseudocallitriche are all schizogenetic[3]. In the petioles of the Marantaceæ the arms of the very loose stellate-lacunar bands are often finally torn asunder by extension of the surrounding tissue, so as to form continuous air-passages, while their torn, often pointed and thick-walled ends rise free into the cavity. In the halms of Scirpus lacustris[4] the meristem differentiates first into prismatic bands of stellate-lacunar tissue, and plates of dense parenchyma, usually one layer thick, which separate these, and appear in transverse section as a net with angular meshes. The stellate cells follow the surface-growth of the latter, their arms elongating greatly, but finally they are for the most part broken up, and only dried remnants are left behind in the prismatic spaces. For further examples comp. infra.

As examples of the substitution of one form for another in a similar position in allied plants the above-mentioned halm of Scirpus lacustris and that of Papyrus may be cited. The latter has air-passages with very similar distribution, but of apparently purely schizogenetic origin; I have however at hand no direct observations on their development. Carex arenaria has in the inner cortex of the rhizome a circle of large air-passages, separated by many-layered, radial lamellæ of parenchyma; these, as is the rule in the Cyperaceæ, are lysigenetic: C. disticha has in the same place 7–10 circles of narrow schizogenetic passages, separated by simple layers of cells.

As regards the *form* of the larger air-cavities it has already been indicated that they are either short polyhedral chambers, e. g. in the leaves of Pistia, the swellings of the petiole of Trapa, and in the Lemnas, or elongated prismatic canals or passages, and this is usually the case in elongated parts, such as stems, petioles, or narrow foliage leaves. The latter but rarely traverse the whole of the elongated part

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[1] Trécul, *l. c.* p. 166.
[2] Compare Frank, *l. c.*
[3] Compare Hegelmaier, Monogr. v. Callitriche, p. 24, Taf. I.
[4] Frank, *l. c.* p. 147.

continuously—e. g. the petiole of Nuphar luteum, according to Frank; they are usually divided into chambers by numerous transverse plates, or diaphragms, which will be described below, or, in the case of stems, are interrupted, at least at the nodes, by plates of parenchyma.

The *structure of the walls* of large air-cavities shows many notable phenomena. Stem, leaves, and also roots of many water and marsh plants are traversed by numerous passages or chambers, and these, especially the schizogenetic ones, are separated in most cases only by plates of parenchyma one layer of cells thick: it is only where vascular or fibrous bundles traverse them that these septa are several or many layers in thickness. Meyen[1] has drawn attention to the fact that the cells of the one-layered lateral septa are often quite uninterruptedly connected over large areas, a condition which seems in fact to be frequent, e. g. in the stems of species of Potamogeton and Myriophyllum, the stems and leaves of Papyrus, Scirpus lacustris, the petioles of the Nymphæaceæ, and of Pontederia crassipes; according to investigations already made, I cannot join in this statement with full certainty: in the first place, because of the great difficulty of proving beyond doubt the absence of very small interstitial spaces, and in the second, because the passages in the petioles of Ceratopteris and Villarsia parnassifolia communicate one with another by very narrow spaces, and those in the internodes of species of Marsilia even by rather large ones. An indirect communication of the passages occurs also where the sides are thus completely closed, through the interstitial spaces in the leaf-lamina, the nodes of the stem, and in certain cases through special diaphragms to be described below.

Schizogenetic spaces are limited by the smooth membranes of the cells which form their wall. In many large passages, e. g. Nuphar[2], or even in cavities, e. g. Rhizome of Aspidium Filix mas, these are covered by a delicate cuticle. It remains for further investigation to decide how far this phenomenon is of general occurrence.

The wall of the lysigenetic spaces is as a rule more or less covered by the remains of those disorganised cells, at the expense of which the space originated, or the latter is here and there loosely filled with remnants of cells. Various special forms originate in connection with this, according as the transitory cells are mechanically torn asunder, or are broken down, or dried up, or according as these several phenomena are combined.

In the pith of most internodes of stems, which become hollow, i. e. perforated by a large, axile, lysigenetic air-passage (Grasses, Umbelliferæ, Compositæ, Equiseta, &c.), the formation of the hollow begins by those transitory roundish or polyhedral cells, which do not follow the growth of the tissue surrounding them, becoming first separated from one another, so as to form schizogenetic cavities which gradually increase in size. The cells of the tissue thus broken up then gradually lose their protoplasm, dry up, and coalesce to flaky or membranous masses, which are attached to the wall of the cavity. The whole process begins in an internode, either simultaneously at many points in the pith (e. g. Phragmites), or in the middle line, spreading centrifugally outwards from it (e. g. Cicuta virosa, peduncle of Taraxacum[3]).

Essentially the same process, on a smaller scale, occurs in the small air-passages which alternate with the vascular bundles in the internodes of Equisetum: also, according to

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[1] Physiol. I. p. 295. [2] Frank, *l. c.* p. 155. [3] Frank, *l. c.* p. 145.

Frank, in those which alternate with the bundles in the leaf-sheath of many grasses, the leaf-sheath and lamina of species of Carex, Luzula maxima, and albida. In the last-named cases however, a further and slightly different condition seems to obtain, which may be observed in the passages in leaves of Liliaceæ, and Amaryllidaceæ, Pandanus, and apparently in many other places: the group of cells, which occupies the place of the future passage, first loses its protoplasm, the membranes become apparently thinner, are partially dissolved, and are finally ruptured by extension of the surrounding tissue. Thin very obscure tatters of the ruptured tissue clothe the walls of the mature passage.

The above-described phenomena are modified in the halms of Cyperaceæ (Scirpus lacustris, species of Heleocharis, and Eriophorum), Juncus effusus, &c., in the leaves of Iris pseudacorus, Sparganium Typha[1], &c., in the following way: the strands of tissue, which originally occupy the cavity of the air-passages, become at first lacunar, with many armed cells, and for a time follow the growth of the surrounding tissue, while the arms of the cells are much elongated: finally they dry up, and are partially broken down. The extreme delicacy which they finally assume indicates that the membranes are partially dissolved. As the result of the phenomena described, groups of distorted, more or less collapsed 'stellate' cells are to be found on the walls of these air-spaces, or even, as in halms of Juncus, the whole cavity is loosely filled with such cells. It is instructive that these cases correspond closely on the one hand to those described above for the Marantaceæ, where many-armed lacunar bands are partially torn away, though their cells do not die: on the other that the dried-up lacunar pith of Juncus corresponds to the numerous cases, where the pith soon dries up to form a cylinder filled with air, without the formation of large cavities or passages.

Finally, in a number of Cyperaceæ those cells, at the expense of which the air-cavity is formed, retain, at least in part, a firm wall, and these walls approach one another, by reason of the tension caused by the surrounding tissue, till their lumen disappears. These collapsed walls are then stretched in the air-cavity like thin plates or threads, which, as Schwendener says, give quite the idea of a glass tube drawn out in a lamp. Schwendener[2] describes such a structure in the case of the many-armed cells in the halm of Scirpus maritimus. The same occurs in the cylindrical-prismatic cells of the cortex of the root of species of Carex and of Cyperus alternifolius: also, though in a slightly developed form, in the air-spaces of the rhizome of Carex arenaria. In the inner cortex of the root of Carex folliculata, for instance, numerous radial bands, 1–3 rows of cells in thickness, continue to be composed of cylindrical-prismatic parenchymatous cells containing starch throughout the tangential extension of the outer cortex: bands, usually of 2–4 rows, alternating with them, are widened out to cavities, in which the membranes of the transversely distorted cells are stretched as almost solid thin plates in a tangential direction.

As has been already indicated, and will be further stated in later chapters, layers of parenchyma alone take part in the formation of the wall of the air-passages in question — that is, if we leave out of account those hair-like single fibres, which spring in certain cases from the wall. The only known exception occurs in the petiole of Thalia dealbata[3], in which each air-passage is traversed throughout its length by numerous thin bundles of sclerenchyma, which for the most part stand quite free in the passage, and are only connected laterally with other elements where they run quite straight through the two sorts of Diaphragms to be described below. Further, it may easily be recognised in the mature plant that the denudation of the bundles is the result of breaking up of the lacunar band of parenchyma, which originally fills the passage, this not keeping pace in its growth with the extension of all the other parts.

[1] Frank, *l. c.* p. 148.

[2] Mechan. Princip. p. 92, Taf. X. 10.

[3] Duval-Jouve, Diaphragmes vasculifères des Monocotylédones, Mém. Acad Montpellier, 1873, p. 168.

Sect. 52. During the formation of longitudinal air-passages, whether they are formed simply schizogenetically or by destruction of cells, transverse zones, which follow the extension, remain connected at certain places, as *diaphragms*, which break the continuity of the passage.

In the first place, they occur in the nodes of all hollow stems, and here they are deep many-layered discs of dense parenchyma, through which vascular bundles, milk-tubes, and secretory passages run, and pass out into the leaves, as will be described in later chapters. In the internodes the large, simple, axile cavity of the hollow stem is uninterrupted, at all events in most cases, and the same holds for the numerous peripheral passages in the internodes of many water-plants, as Ceratophyllum, Myriophyllum, Hippuris, Elatine Alsinastrum, species of Jussiæa, Limnanthemum nymphoides, Zostera, Posidonia Caulini, Nelumbium: also, with a restriction to be given below, for the leaf- and flower-stalks of the native Nymphæaceæ: and lastly, for all roots with large air-passages, though these require further investigation in this respect. On the other hand the air-passages in the internodes, petioles, and leaves of most Monocotyledons, the petioles of Limnanthemum nymphoides, the internodes and petioles or conical leaves of the Marsiliaceæ, the leaves of the Isoeteæ, &c., are partitioned by diaphragms.

These are separated by short distances, usually a few millimetres, rarely over 1^{cm}, from one another; they are horizontal or oblique; they may alternate, those of adjoining passages being at unequal heights, or they may be at about the same height, so that one and the same diaphragm extends evenly over several or many passages.

The diaphragms consist of one, more rarely of several layers of parenchymatous cells, often rich in chlorophyll, between which air-containing interstitial spaces always lead from one chamber into another: they are sometimes composed of dense parenchyma with narrow interstitial spaces, as e.g. in the leaves of Luzula maxima which has diaphragms two layers thick, in species of Carex, Cladium Mariscus, Scirpus sylvaticus, maritimus, Cyperus fuscus, Veratrum album, Iris pseudacorus, Posidonia Caulini, Zostera, Caladium, Colocasia and its allies, &c.; others consist of many-armed cells, connected by the ends of the arms, and forming a plate with wide lacunæ, as in the leaves and stems of many water-plants, Isoetes, Potamogeton, Aponogeton, species of Typha, Sparganium, Pontederia, Butomus, Sagittaria, and Alisma, petioles of Limnanthemum, Strelitzia, halms of Papyrus, Heleocharis palustris, Eriophorum, leaves of Pandanus, &c. In the wide central portion of the halm of Juncus effusus, glaucus, and their allies, transverse zones of some few layers of many-armed stellate cells keep their walls relatively firm, and persist as diaphragms, while the delicate tissue between them, which is also many-armed and lacunar, collapses.

Intermediate forms, which make it impossible to separate the lacunar diaphragms sharply from the dense ones, are not uncommon: for instance, those composed of short-armed cells, with narrow cavities between, in Scirpus lacustris, in the leaf-sheaths and leaves of Glyceria aquatica, and Oryza sativa (Duval-Jouve), to which many of those above-named correspond; and the narrow-lacunar diaphragms of the Marsiliaceæ, the structure of which is not unlike that of the lateral walls of the air-passages, &c.

Two sorts of diaphragms were mentioned above in the case of the air-passages

of the petiole of Thalia dealbata. The first are lacunar plates, consisting of many-armed cells usually one layer in thickness, which have apparently resulted from transverse rupture of a band of similar tissue, which originally filled the passage. The others consist of a layer of relatively small-celled, dense parenchyma, which is covered on each surface by a lacunar layer of many-armed cells. Similar conditions of undoubtedly similar origin are found in the petioles of species of Musa.

In the leaves and petioles of the Monocotyledons above named, and the halm-internodes, which resemble them in structure (Scirpus, Juncus, Papyrus, &c.), and further in the petioles of Nelumbium, the longitudinal bundles are connected by more or less numerous thin transverse branches (Sects. 66, 91). These run through the diaphragms, especially where the lateral walls of the air-passages are only a single layer of cells in thickness, either transversely through their surface, or through their margin, which abuts on the lateral wall. If the diaphragms are one layer of cells thick, the vascular bundle appears as a swelling of it, several layers in thickness, which may protrude either on both surfaces (e.g. Sagittaria), or only on one (e.g. Scirpus lacustris). Either all the diaphragms contain a transverse bundle (e.g. Papyrus), or this is the case with some of them and not with others (e.g. Pontederia, Butomus): of the two sorts in Thalia and Musa, only the dense ones contain bundles. Where all the longitudinal corners between the air-passages do not contain longitudinal bundles, as in Papyrus, Sagittaria, and the leaf of Acorus Calamus, the diaphragms with transverse bundles must be continuous transversely through several passages, their arrangement is thus to a certain extent dependent upon that of the vascular bundles.

The form of the cells of lacunar diaphragms with many-armed cells, which has been studied as a hobby by some[1], is particularly various, and often beautiful in diaphragms one layer thick, in which all the arms of the cells lie in one plane. For details reference may be made to the works cited, while here some few of the chief forms from stems and petioles will be noticed.

(1) Rather regular stellate cells with long arms, having between them wide lacunæ, which usually correspond to the original corners of contact of three or more cells, e. g. Isoetes, Villarsia, Nelumbium, Potamogeton natans, Thalia, Pandanus, Pontederia, Eriophorum, Heleocharis palustris, &c. In the two latter the lacunæ are bordered by the arms of three cells, in outline they are rounded triangular, and contracted in the middle by the swollen margins of the surfaces of contact of the pair of arms forming each side: they have thus the form of a gothic trefoil, and the whole diaphragm has, owing to this, and to the delicate pitting of its thick cell-membranes, a peculiar appearance.

(2) Short-armed cells (*a*) with rounded lacunæ, corresponding to the original corners (e. g. leaf of Sagittaria sagittifolia, Butomus).

(*b*) With a series of small round or slit-like lacunæ along the original limiting surface of two cells: Scirpus lacustris.

(*c*) With lacunæ at both places, those corresponding to the corners being larger than those along the sides (e. g. Sagittaria indica, lancifolia), or both being of almost equal size (e. g. Marsilia).

In the diaphragms of Scirpus lacustris the condition described under (*c*) occurs,

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[1] Meyen, Phytotomie, pp. 85, 193.—Haarlemer Preisschrift, p. 138, &c.—N. Syst. d. Pflanzenphysiologie, I. p. 294, &c.—Duval-Jouve, *l. c.*

especially at the margin, often with relatively very large cavities at the corners (comp. Meyen, Physiol. I, Taf. II, Figs. 3 & 4). The greater part of the surface of these diaphragms has, on the other hand, the following structure as a rule. The surface appears divided into polygonal areas, and each of these is again divided by parallel walls (which may be termed the inner walls) into 4 cells on the average, of which the central ones are narrow and quadrangular, the outer are irregular and narrow, with 3–5 corners. The inner walls of an area are usually not parallel to those of the neighbouring areas. The walls which limit the areas, and apparently correspond to those of the mother cells which are subsequently divided by the inner walls, are irregularly undulated and uninterruptedly connected with those adjoining them. But along the parallel inner walls each of the cells has a row of usually 5–7 short arms, and between these are roundish quadrangular cavities.

The several-layered lacunar diaphragms naturally resemble in the main points the masses of stellate-lacunar parenchyma above mentioned. Those only of the halm of Papyrus, which run transversely, though slanting and distorted, through many air-passages, deserve special mention, on the one hand, because of the extremely irregular form and arrangement of the arms of their cells, on the other, because their lacunar tissue is also continued transversely through the lateral walls of the air-passages, from one to the other, and from the outermost into the peripheral chlorophyll-parenchyma. Since all diaphragms, or at least most of them, are continued transversely through several or many air-passages, all the passages communicate, by this arrangement, indirectly one with another, with the air-containing interstitial spaces of the chlorophyll-parenchyma, and through this with the stomata, though in the lateral walls of the passages themselves no interstitial spaces are to be found.

In such plants as secrete much calcium oxalate, not only is it often laid up in large quantity in the form of small crystals in the cells which adjoin the air-passages, as e. g. in the diaphragms of Musa and Sagittaria, but the structure of the walls, both laterally and on the diaphragms, is often complicated by the intercalation of crystal-containing sacs in the layer covering the walls, or these are seated upon the above layer as papillæ or small hairs. As far as is known this only occurs in schizogenetic, not in lysigenetic spaces: it remains for observations of the development to decide whether Nelumbium, with its numerous grouped crystals, which protrude into the air-spaces, is an exception to this. Of the forms of crystal-containing sacs described in Sect. 32, we have here to deal more especially with elongated or spindle-shaped sacs with raphides, and spherical sacs, each one enclosing a single stellate group of crystals.

Such of these as are intercalated in the layer covering the walls require no further mention here. The sacs with clustered crystals which protrude into the cavity are always seated on the wall, singly or (Trapa) in groups, as small round bladders with a broad base. When old their membrane, which is always delicate, is in many cases extremely thin and difficult to see—it remains doubtful whether it entirely disappears or not—so that the clusters project or appear to project freely into the cavity.

The projecting, elongated or spindle-shaped raphide-cells are sometimes attached to the lateral walls, in which case they either have one of their ends inserted on it, or are attached by the middle to a narrow surface of a cell of the wall, while the two ends project freely upwards and downwards into the space. The same holds sometimes for the one-layered diaphragms, and the walls of the chambers (also one layer of cells thick) in the leaf of Pistia; sometimes in this plant the raphide-cells have

their middle part intercalated in the plate of cells, while their ends extend over it, the one upwards, the other downwards.

As examples of all these conditions in sacs with clustered crystals may be cited Myriophyllum, Trapa, Nelumbium: in raphide-sacs, Pontederia[1], Scitamineæ, Philydrum[2], Colocasia odora: in both forms together, many Aroideæ, as Colocasia antiquorum, Caladium nymphæifolium[3], Pistia.

In the diaphragms of the petiole of Pontederia (P. cordata and crassipes) there are found, besides the raphide sacs, others, of spindle-like shape, with their longer axis placed at right angles to the diaphragm, and with their middle intercalated in it, so that the ends project upwards and downwards into the space: each of these contains a single spear-like crystal sharply pointed at both ends. This, together with the sac which contains it, attains a length, especially in P. cordata, of more than three times the thickness of the diaphragm. Finally, the membrane of the sac covering the ends of the crystal ceases to be apparent, so that the latter seems to protrude freely into the air-space[4].

Sect. 53. The walls of many large lacunæ and air-passages are characterised by projecting cells or portions of cells, which, from their form, are termed *hairs*. These may be divided into two categories, namely, glandular hairs; and non-glandular, usually firm hairs like sclerenchymatous fibres. The only forms of the first category are those glandular hairs, first noticed briefly by Mettenius[5], and described later by Schacht[6], in the air-cavities of the rhizome and base of the petiole of Aspidium Filix mas. One or more unicellular capitate hairs, which are seated singly on adjoining starch-containing parenchymatous cells, project into the larger cavities of this plant: they arise originally as daughter-cells of the latter, or as outgrowths of them. The small thin cylindrical stalk widens out into a large pear-shaped head, and this secretes on its surface, as far as the limits of the stalk, a firm, greenish, brilliant, thick layer of resin. The mode of its secretion and the structure of the whole hair are the same as above described for the *glandular hairs* (p. 88); glandular hairs, which closely resemble these intercellular hairs, occur here and there on the surface of the bases of the petioles of the male fern, as teeth of the base of the Paleæ. In the base of the petiole of Aspidium spinulosum—and probably also of other allied species—such internal, intercellular glandular hairs are found, though in less numbers than in Filix-mas.

Intercellular hairs of the second category occur especially in the air-passages of such plants as have no diaphragms: Pilularia, Nymphæaceæ, Aroideæ, Rhizophora, also Limnanthemum. As may be judged from their structure and arrangement, they, like the diaphragms, serve as a support. Russow[7] found in the air-passages of the root of Pilularia globulifera hairs rolled up like watch-springs, with thin membranes, studded with fine external warts: their arrangement is as follows. The inner cortex contains 12 air-passages separated by radial lateral walls one layer of cells in thickness; 6 broader ones alternate with 6 narrower ones. Single cells of the lateral

[1] Meyen, Phytotomie, Taf. V.
[2] S. F. Hoffmann, Linnæa, XII. p. 683.
[3] Meyen, *l. c.* Tab. XII.
[4] Compare Meyen, Phytotomie, Taf. V.—Duval-Jouve, *l. c.* p. 166.
[5] Fil. horti. Lips. p. 92.
[6] Pringsheim's Jahrb. III. p. 352.
[7] Vergl. Unters. p. 22.

walls, which adjoin the outer cortex, elongate to form these hairs: they protrude as blunt sacs, with $1\frac{1}{2}$ narrow turns, into the small passages, filling up the breadth of the passage: they all curve in the same direction. The vertical distance between two hairs is never less than the greatest diameter of the narrower passages.

In the air-passages of the leaf- and flower-stalks of the *Nymphæaceæ*, in species of Nymphæa (but not Nuphar), and, according to S. Hoffmann, also in the roots and Rhizome, there have been known, since the time of Guettard[1], branched 'stellate hairs' with pointed arms, and a firm wall, which shows numerous blunt, wart-shaped, external thickenings, containing calcium oxalate[2]. In the petioles and peduncles the hairs arise from the simple perpendicular rows of cells, forming the corners of the air-passages, which appear polygonal in transverse section: they are at different heights one above another, often being separated from one another in one corner by only few cells; in neighbouring ones they are at different heights, so that on each large transverse or longitudinal section several may be seen at once (Fig. 88). A cell of the corner series, flattened above and below, puts out an arm into each of the air-passages (usually 3, more rarely 4) which adjoin it: these, directly they enter the passage, divide into the diverging pointed branches of the permanently unicellular hair. In the simple regular case, as is most common in the petiole of Nuphar pumilum, each arm branches once into two almost equal branches, of which one turns upwards, the other downwards. In N. luteum this vertical branching is often immediately succeeded by a second at right angles to it, so that in the most regular case each arm runs out into four pointed branches, two diverging obliquely upwards and two obliquely downwards. But in this, as in other species, it often happens that, by the absence of one of them, or unequal development of the branches of this second bifurcation, a more irregular general form is attained: also a more complex branching may occur. In the larger air-passages the branches are shorter than the diameter of the passages; they diverge almost at right angles, and as a rule they do not touch the wall of the passages. In the narrow passages, like those of the periphery of the petiole of the above species, and, according to Meyen, in all cases in Nymphæa odorata and cærulea, the hairs are not at all or only slightly smaller than in the wide ones; they therefore frequently touch the lateral walls. The angle of divergence of

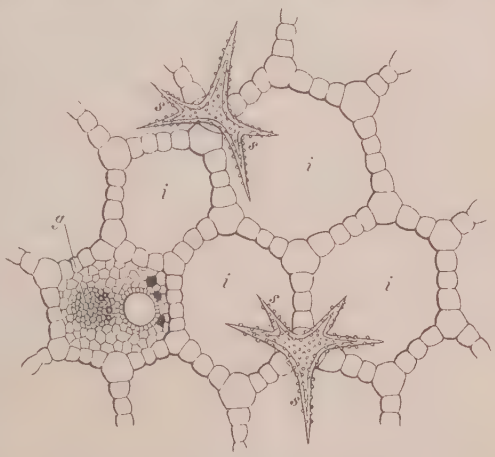

FIG. 88.—Nuphar advena: transverse section through the petiole; *g* vascular bundle, *i* air-passages, *s* stellate hairs. From Sachs' Textbook.

[1] Compare Meyen, Physiologie, I. p. 311; Phytotomie, p. 200, Taf. IV.—Trécul, Ann. Sci. Nat. 4 sér. tom. IV.

[2] According to a note by H. von Mohl, communicated to me.

their vertical branches is often much greater than in the above, reaching not uncommonly 180°, so that the hair appears in profile in the form of a letter H.

In the lacunæ of the lamina the form of the hairs in the portion near the lower surface does not differ essentially from that above described. At the limit between this and the lamellar layer of parenchyma of the upper surface are found numerous hairs, which put out diverging arms both downwards into the lacunæ, and also upwards: these run straight and perpendicular between the lamellæ of parenchyma, as far as the inner surface of the epidermis[1].

In the air-passages of those Nymphæaceæ which have been investigated, at least in those of the petiole, there occurs another sort of hair formation, different from that described. Single cells of the lateral wall put out into the passage a sac-like outgrowth, which branches frequently and irregularly to form many arms, and is divided by septa into cells, which are also irregular and many-armed. The same growth continues in these for a long time, so that a small lacunar mass of cells is formed, which loosely fills up the passage like a diaphragm of many layers of cells. The cells of these pseudo-diaphragms have permanently delicate, smooth walls, and scanty protoplasm with some few starch-grains[2].

Hard stellate hairs with pointed arms, resembling closely those of the Nymphæaceæ, are found in the air-passages of Limnanthemum nymphoides, and other investigated species of the same genus, in stems, rhizomes, and petioles[3]. They are always distinguished from those of the Nymphæaceæ by their smooth membranes; many protrude only into a single air-passage. These stellate hairs have not hitherto been found either in the true Villarsias, or in other Menyantheæ, or in other water-plants of like habit.

In certain Aroideæ, viz. the group of the Monsterineæ (Monstera, Tornelia, Heteropsis, &c.), Pothos Rumphii, and Spathiphyllum[4], numerous hairs of this sort are contained in the cavities and passages of the lamellar parenchyma. They usually occur in all parts of the plant, or they are absent in certain parts, e. g. the rhizome and the roots of Spathiphyllum. They arise by early outgrowth of a cell of the wall of the cavity (usually one layer of cells thick) which remains relatively narrow, so as to form long, thin pointed arms. In the longitudinally elongated cavities of internodes, petioles, and roots more simple forms occur as a rule: each hair-cell grows out into one, two, or rarely three of the adjoining passages, forming in each two arms of equal or unequal length, and tapering very gradually to a point: these diverge exactly 180° from their point of origin. The hair thus assumes the form of a spindle-shaped body, with a short blunt transverse appendage, which is fastened in the lateral wall of a cavity: or of an H with a short transverse portion, which is imbedded in the lateral wall between two cavities (Fig. 89). Of the many irregularities which occur in this type, only one need be mentioned here, viz. that an arm may put out single lateral branches, which enter like hooks into neighbouring lacunæ. In the

[1] Meyen, Haarlemer Preisschr. Taf. V; Physiol. *l. c.* p. 312.—Trécul, *l. c.* pl. 12, fig. 25.

[2] Trécul, *l. c.* fig. 12.—Frank, *l. c.* p. 153.

[3] Grisebach und Hoffmann, Linnæa, Bd. XII. p. 681.—S. F. Hoffmann, Ibid. Bd. XIII. p. 291 (1839).

[4] Van Tieghem, Structure des Aroidées, *l. c.* p. 137, &c.

short lacunæ of the lamina, which communicate in all directions, the branching of the hairs is more complex and irregular; they here put out radiating arms diverging on different sides, which themselves again branch, and may traverse many lacunæ. Each lacuna, especially in stems and petioles, is thus permeated by numerous hairs; they may be found in every transverse section, either singly or many—up to 10 or 20—in one cavity, in the latter case side by side, but always without touching one another. The size and stiffness of the hairs varies to a certain extent in special cases: in Spathiphyllum lancæfolium van Tieghem found them the longer, narrower, and more thin-walled, the more numerous they were side by side. Their length is very considerable: in the last-named plant it reaches 5–7^{mm}, with an average width of 0.01^{mm}.

The membrane of these hairs is always colourless, quite smooth, more or less thickened, and stratified; the inner layers, when the wall is of great thickness, have shallow pits: their cavity is usually uninterrupted, rarely it is partitioned by a few thin septa: the contents are transparent and watery, with isolated granules, and sometimes small crystals of calcium oxalate. They closely resemble sclerenchymatous fibres, and were therefore at first described as 'bast-cells'[1].

The occurrence of intercellular hairs, quite similar to those of the Aroideæ, in the pith and cortex of species of Rhizophora, is very remarkable. They are here usually of the H form, on the whole harder than in the Aroideæ, and their arms are usually solitary, though sometimes 2–4 occur in one intercellular passage, filling it loosely.

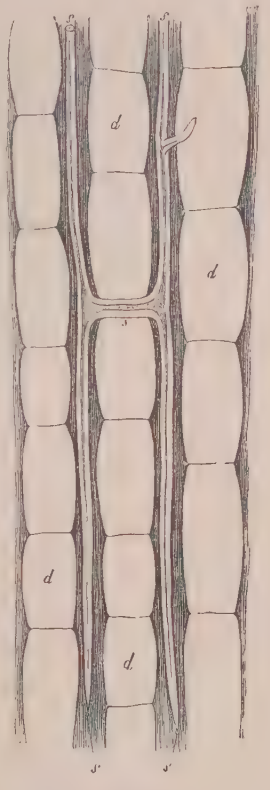

FIG. 89.—Monstera deliciosa; longitudinal section through the petiole. *d*, *d* parenchyma; *s*—*s* a hair in form of an H, the main arms running perpendicularly through the air-spaces; at the top to the right is a small curved branch. From Sachs' Textbook

It is instructive that the above-described many-armed hard-walled hairs of the Nymphæaceæ, Limnanthema, Aroideæ, and Rhizophoras are fundamentally related to sclerenchymatous fibres, in every respect, and are only special cases of the latter, distinguished by their form and distribution, and that thus their earlier designation as 'bast-fibres' was not without justification, provided sclerenchymatous-fibres were really meant by this name. Comp. Sect. 30.

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[1] Schleiden, Wiegman's Archiv, 1839, Bd. I. p. 211.—Beiträge, p. 42.

PART II.

THE ARRANGEMENT OF THE FORMS OF TISSUE.

FIRST SECTION.

PRIMARY ARRANGEMENT.

Sect. 54. The different forms of tissue result from the differentiation of the primary meristem present in the growing points, and have a definite relative position and arrangement. In very many instances this is permanent, as is the case in leaves, and in the stems and roots of plants not belonging to the Dicotyledons and Gymnosperms. In other cases, especially in the last-named plants, either new structures, which arise from secondary meristems, are formed, in addition to the tissues derived from the primary meristem (p. 4); or changes, which are consequences of secondary formations, appear in the primary tissues.

The masses of tissue directly derived from the primary meristem and their arrangement are called *primary* to distinguish them from those of later *secondary* origin, and from consecutive secondary changes. We shall here study, in the first place, only the first category. It is, it is true, to be expected *a priori*, that the development of the primary masses of tissue takes place not suddenly, but in definite succession, and that the secondary changes may be closely connected with it, without there being any sharp limit between the two processes. Nevertheless in many typical cases a definite limit between them can be found, and, from these as a starting-point, it can be extended to all.

The course of treatment in this section has been generally indicated by the distinctions drawn in the first part. Of the forms of tissue there distinguished, the epidermis will naturally not be treated of further. Its arrangement can be concluded from Chap. I. 1: also the arrangement of single parts of it, which should properly

be reproduced here, had to be described above, and may be there referred to if necessary. Peculiarities, which depend upon the tissues covered by it, will be noticed when the latter are treated of.

As regards the other forms of tissue, to be dealt with in this section, we may refer in the first place to the method of grouping given on p. 5, which holds for all tissues. It may here be added that a group of tissues bordering directly on the epidermis is called from its position *hypodermal*, while distinct hypodermal layers are indicated by the substantive *hypoderma*[1].

It is best to begin the description of the primary arrangement of tissues with the tracheæ and sieve-tubes, since these are connected, in almost all plants with which we shall be engaged, into strands or *vascular bundles;* and these form a well-marked, uniformly comparable skeleton, on and around which the other tissues arrange themselves.

[1] Pfitzer, Pringsheim's Jahrb. Bd. VIII.

CHAPTER VIII.

TRACHEÆ AND SIEVE-TUBES.

1. *Tracheæ and sieve-tubes outside the vascular bundles.*

Sect. 55. Both the above organs are, as above indicated, united as a rule to form the vascular bundles. They occur however, in many special cases, external to and side by side with the latter in other regions also, and otherwise distributed.

Scattered tracheides occur outside the vascular bundles, enclosed in other tissues in the stems and scale-leaves of species of Salicornia and Nepenthes[1], and in the base of the leaf of the Isoeteæ.

In the many-layered, chlorophyll-containing parenchyma of the cortex of the stem of those species of Salicornia which were examined, Duval-Jouve[2] found, according to the species, cylindrical or spindle-shaped tubes, which have exactly the structure of air-containing tracheides. They are about as long as the chlorophyll-containing layer of the cortex is thick, and have their longer axis perpendicular to the epidermis, which they do not reach, but end one layer of cells further in, close to one of the very numerous air-cavities of the stomata. Their other end is in contact with the colourless inner parenchyma of the cortex, but does not extend to a vascular bundle. In S. sarmentosa, patula (= S. herbacea of most authors), and fruticosa, the tracheides are rather regularly cylindrical-spindle-shaped; their completely colourless wall is thickened at the sides with a close and fine spiral fibre, on the blunt ends it is smooth. In S. Emerici Duval-Jouve found the tracheides but few, and weakly developed. In S. macrostachya they are irregularly spindle-shaped, with lateral, short, pointed excrescences, and often with hooked ends; their membrane is uniformly and strongly thickened, it is smooth or scarcely pitted; they remind one to a certain extent of the rod-shaped sclerenchymatous cells in the leaves of Proteaceæ (comp. p. 130 and Chap. X).

The tracheides of the species of Nepenthes[3], which are also filled with air, are almost cylindrical, usually a little tapered at the ends, and of varying length, which however hardly exceeds that of 10–20 cells of the parenchyma. Their colourless wall has a close and delicate spiral thickening. They occur in the stem, distributed in all parts of it, and in large quantity in the parenchyma; similarly in the petiole and

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[1] [Cf. Mangin, Développement des cellules spiralées. *Ref.* Bot. Centralbl. 1882, Bd. XII. p. 85.]

[2] Des Salicornia de l'Hérault, Bulletin de la Société Bot. de France, tom. XV. p. 140, pl. 1.

[3] Korthals, Verhandelingen over de Naturl. Geschied. d. Nederl. overzee. bezittingen; Botanie, p. 1.—Compare also Unger, Grundlinien, p. 11.

lamina, and in the pitchers 2–3 layers of cells below the surface. They are never continuous with the vascular bundles. In the stem they are all arranged parallel to its axis; in the leaf, at least in the wall of the pitcher-shaped portion, they point irregularly in different directions.

In the base of the leaf of the Isoeteæ [1] are found series of short spiral tracheides, having the same form as those of the xylem in the stem of these plants: they occur in the dense mass of parenchyma at the point of insertion of the membranous ligula, called by Braun the Glossopodium. They extend from the upper and lower margins of this body almost horizontally to the inner surface of the base of the leaf: those of the upper side towards the posterior wall, those of the under side towards the membranous lip-like lower margin of the depression in which the ligule is seated. They have no connection with the vascular bundle of the leaf.

Sect. 56. A continuous layer of air-containing tracheides covers, as a *sheath* or *velamen*, the aerial roots of epiphytic orchids, which in this respect resemble those of some other plants, especially Aroideæ.

The tracheal sheath of the roots of Orchids is produced from the layer of dermatogen, which, according to Treub [2], in Vanilla and Stanhopea, is differentiated close behind the growing-point from a common initial group for the root-cap and the body of the root: this I found to be the case in Vanda furva, while in species of Oncidium (Fig. 90, 91) the dermatogen passes over the growing-point as a distinct layer between periblem and calyptrogen. The simple layer of the periblem, adjoining the dermatogen internally, develops into the endodermis, which consists of longitudinal rows of alternately elongated and short cells (comp. p. 125).

The very delicate cuticle which is present at first, i. e. where the root emerges from the root-cap, is absent over the mature outer surface, or at least cannot be proved to be present as a continuous skin.

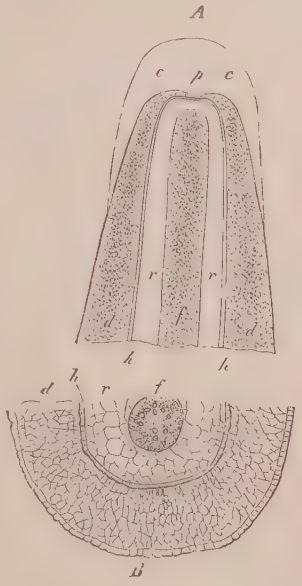

Fig. 90.—Species of Oncidium; aerial root, slightly magnified. *A* axile longitudinal section through the apex, *c* root-cap, *p* depressed centre of the growing point, *d* sheath of tracheides, *h* endodermis, *f* vascular bundle, *r* cortical parenchyma. *B* transverse section through a mature part; lettering as in *A*.

The sheath of tracheides remains in some few cases a single layer (Vanilla planifolia, aphylla, Sarcopodium Lobbii, Cirrhopetalum Wallichii): in most cases it is cut up by corresponding divisions, which begin behind the growing-point, into several layers, numbering according to the species 2, 3, 6, or 18 (Cyrtopodium spec.). All its elements are in uninterrupted connection with one another (comp. Figs. 90, 91, *d*). The single tracheides are approximately iso-diametric, or slightly elongated

[1] Mettenius, Linnæa, 1847, p. 272.—Hofmeister, Beitr. p. 151.—A. Braun, Isoeten d. Ins. Sardinien, Berliner Acad. Monatsbr. 1863, p. 571.

[2] *l. c.*, compare p. 10.

in the same direction as the root. Their membranes are usually colourless, thus the surface of the air-containing layer appears white and shining. In water, which it quickly absorbs, the layer becomes transparent; the internal green cortical parenchyma then becomes apparent. Another cause of the green colour is that in old roots (Vanda furva and Anselia africana, according to Leitgeb) small green algal cells sometimes enter the cavity of the tracheides. When old, the air-containing layer is in many species entirely thrown off (Angræcum subulatum, Cymbidium ensifolium, Zygopetalum Mackai, according to Leitgeb; also Vanda furva), or only the innermost layer remains: the result of this also is that the green colour of the cortical parenchyma becomes visible.

In Eria stellata the colour of the aerial roots is brown, since the membranes of the tracheides assume a brown colour: in Trichotosia ferox the tracheides of the

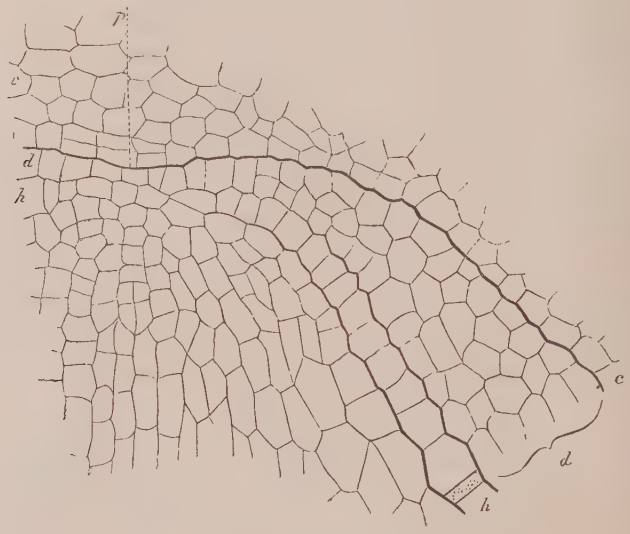

FIG. 91.—Median longitudinal section through the apex of a young root of the same Oncidium as Fig. 90, with the same lettering (375).

four-layered sheath are filled with a reddish-brown mass, which gives the roots a reddish-brown colour; the same sometimes applies to Cymbidium marginatum. Larger or smaller masses of a loosely coherent black-brown substance were found by Leitgeb in many cases, especially in the inmost layer of cells: and in specially large quantity in Renanthera coccinea. According to Leitgeb, those walls which cover the short thin-walled endodermal cells always show a limited brown coloration.

With the exception of these last-named cases, air alone, or water obtained from without, is always contained in the tracheides; the protoplasm and nucleus disappear entirely during their development, close to the growing-point.

During their differentiation the walls of the tracheides, like those of other tracheal organs, become lignified to an extent which varies according to the special case. As regards the form of thickening the greatest variety may be seen, not only in those of different species often closely allied to one another, but also in those of different layers

of the same root, and in the several walls of one and the same tracheide. In most cases the walls are thickened by spiral fibres, which in some plants run exactly parallel (Sarcanthus rostratus, Gongora Jaenischii, Brassia maculata, Cattleya Mossiæ), or leave slits between them (Oncidium pulvinatum, flexuosum, sanguineum), or form large meshes (Epidendron elongatum, Brassia caudata): or in other cases are arranged in band-like groups (Cyrtochilum bictoniense). According as these fibres are in close juxtaposition (Oncidium flexuosum, sanguineum, Cymbidium ensifolium), or are further apart from one another (Maxillaria tricolor, Camaridium ochroleucum), the slits and meshes are smaller or larger. Further, since in many cases the fibres of two contiguous walls cross, the superposed slits and meshes are also crossed. Not uncommonly the spiral fibres, which usually traverse the wall obliquely, but often appear (in transverse sections) radially arranged, run quite irregularly, in which case they are however sparsely distributed and branch repeatedly, and then either continue their course independently, or again unite later to form broad bands (Renanthera matutina, Phalænopsis grandiflora, Saccolabium Blumei). In other cases the spiral-fibrous thickening disappears entirely, and there are only solitary slits to be seen, which are still arranged in spiral lines (Angræcum subulatum, outermost layer); but not uncommonly this spiral arrangement also disappears, and a purely reticulate thickening is found (Dendrocolla teres, Sobralia decora, Vanda furva). In some though less frequent cases the walls are again quite regularly thickened, and only present more or less numerous pits (Angræcum subulatum, second layer); often the thickening layers are only developed at the corners (Sarcopodium Lobbii, Cirrhopetalum Wallichii), or the walls are without any thickening at all, and are quite thin (Trichotosia ferox ; Angræcum subulatum, third layer, Leitgeb).

These examples may serve to show the variety of the details, while reference may be made to the further special descriptions and figures of Oudemans and Leitgeb. What has been said of the triple sheath of Angræcum subulatum shows at the same time the variety of form of thickening, which often occurs in successive layers. Though the conditions in this respect also are very variable, the rule still holds that both in forms with one and with many layers, at least the outer and the inner surfaces are characterised by special thickening of the membranes.

At those points where the spiral or netted fibres separate widely in a slit-like manner from one another, the wall-surfaces which have no fibres are not uncommonly perforated[1], whether they be on the free surface or in the body of the sheath. Thus in the latter case, speaking accurately, the tracheides are united to form vessels. Where the sheath consists of several layers, the elements of the outermost layer often grow out as papillæ or sac-like hairs, a phenomenon which also appears in the one-layered sheath. In those cases known, all the elements of the surface are not engaged in the formation of hairs. The latter sometimes occur on roots which protrude freely into the air, as Leitgeb found in seventeen species of different genera (in Eria stellata the felt of hairs, which is usually dense, is quite absent if the roots grow in moss or earth): while in other cases the formation of hairs appears only when the

[1] Von Mohl, Verm. Schriften, p. 322 (Epidendron elongatum).

growing root is in contact with a solid (damp) body—Epidendron elongatum, species of Stanhopea, Oncidium sphacelatum, flexuosum, Maxillaria Harrisoniæ. The hairs attach themselves firmly to the contiguous body, while not uncommonly they are considerably spread out, their free ends even branching in a palmate manner. The membrane and contents of the hairs resemble those of the rest of the root-sheath of the species. The membrane separates readily into spiral bands: it is easily ruptured in many species (e. g. Vanda furva, Sobralia decora), and thus are formed some of the holes in the outer surface.

The tracheides of the inmost layer are for the most part more elongated than the rest; further they are either of fundamentally similar form and structure all round, or are characterised by peculiarities, where they cover the thin-walled endodermal cells. As regards the peculiarities of form, they appear as one-, two-, or three-layered groups of small flat elements, which are evenly fitted at the points indicated into the other part of the sheath. As regards their structure, the special form of thickening of their walls often differs from that of the surrounding tissue, but within the rules above laid down for the latter. The brown coloration of the limiting walls, which Leitgeb states is constant, but which I failed to see in Vanda furva, Oncidium sphegiferum and Acropera Loddigesii, has been above mentioned. Peculiar thickenings are found in special cases at the points indicated: in Trigonidium Egertonianum a strong stratified swelling intrudes slightly into the cavity of the cell on that part of the wall which abuts on the thin-walled endodermal cells: in the Sobralias there is a similar, very protuberant, almost spherical, stratified swelling of a dark brown colour. The cells of the inmost layer of the sheath are in the latter plants in all cases of fundamentally the same form: one of them overlies one of the thin-walled endodermal cells, or two or three of them are in contact with the latter: since each of the adjoining cells has a swelling of the wall, 1–3 of the latter overlie one thin-walled cell.

The aerial roots of many epiphytic Aroideæ have a sheath of Tracheides derived from the dermatogen, and resembling that of the Orchids in all fundamental points. In Anthurium acaule, egregium, crassinervium, and intermedium, the tracheides have spiral or reticulate fibres: the sheath is 4–5 layers thick. In other species of Anthurium there are 2 or several, in Homalonema cærulescens even 6 layers, but the walls of the tracheides are smooth and thin. A one-layered sheath consisting of thin and smooth-walled elements occurs in Anthurium violaceum, Philodendron pedatum, and other Aroideæ, and again in the aerial roots of Hartwegia comosa Nees. (Chlorophytum Sternbergianum, Steud.), and Hoya carnosa. In the latter cases the air-containing elements (which often grow out to hairs or papillæ) may just as well be called dried-up cells as tracheides, or perhaps better. Still it is more proper to place them here, as incomplete forms, with the sheaths of tracheides, since in those roots on which they occur (as in all others here cited) an endodermis structurally similar to that of the Orchids abuts internally on the air-containing sheath.

The above description of the air-containing sheaths of roots is based on the above-cited works; also on the investigations of *Oudemans*, Ueber den Sitz der Oberhaut bei den Luftwurzeln der Orchideen, Abhandl. d. k. Acad. z. Amsterdam, Math. phys. Klasse IX. 1861, and especially *Leitgeb*, Die Luftwurzeln der Orchideen, Denkschr. d. Wiener

Acad. Math. naturw. Classe, Bd. 24, p. 179 (1864).—Ueber kugelförmige Zellverdickungen in der Wurzelhülle einiger Orchideen, Sitzgsbr. d. Wiener Acad. Bd. 49.—Ueber Hartwegia comosa, &c., ibid. Bd. 49, p. 138.—Also *Nicolai*, das Wachsthum der Wurzel. Schr. d. Physik. Gesellsch. z. Königsberg, VII. (1865) p. 66. The remarkable white 'parchment-like' skin of the Orchids has been known since Link (Elem. philosoph. bot. Ed. I. (1824) p. 395), and repeatedly investigated by Meyen (Phytotomie, p. 163; Physiologie, p. 47): Mohl, Unger (Anatomie u. Physiol. p. 194) in the Orchids, and by Schleiden (Grundzüge, Ed. 3, p. 284) in these and the Aroids: but a clear view of the case was not obtained, since according to Meyen and Schleiden the endodermis was taken for the epidermis (its short cells were regarded by Schleiden as stomata). Schacht (Lehrb. I. p. 258) and Oudemans regarded only the simple, outermost air-containing layer as the epidermis, and the inner layers as an hypodermal 'intermediate' tissue. The statements of Chatin, Anatomie des plantes äeriennes de l'ordre des Orchidées, Mem. Soc. de Cherbourg, Vol. IV, 1856, and of Fockens, Ueber die Luftwurzeln, &c., Diss. Göttingen, 1857, have been corrected by Leitgeb and Oudemans in those points in which they differ from the above description.

Sect. 57. *Sieve-tubes* occur outside the vascular bundles in a relatively large number of stems of Dicotyledons, and of some Monocotyledons: they form small groups or bundles, which traverse the parts longitudinally, and anastomose at the nodes not only with one another, but also with those of the vascular bundles. The tubes are always accompanied by the same delicate, elongated cells, as in the vascular bundles—these will be described when the latter are treated of—often also by sclerenchymatous fibres and milk-tubes.

Many Dicotyledons have bundles of sieve-tubes at the periphery of the pith, near to the ring of vascular bundles, many Melastomaceæ also have them scattered through the pith. In many plants—Myrtaceæ, Daphne, Strychnos, Apocynaceæ, and Asclepiadaceæ, Convolvulaceæ, often also in the families to be named below—they approach so closely to the inner margin of the vascular bundles that they are better to be regarded as parts of these, and in all cases the bundles of the pith are related so closely and in such various ways to the system of vascular bundles that the subject will be returned to when the latter is described: reference may therefore be made to Sects. 62 and 103. Therefore we need only mention here the bundles of sieve-tubes which separately traverse the periphery of the pith in the stems of species of Solanum (S. tuberosum, Dulcamara), Nicotiana, Datura, and Cestrum; of many Campanulaceæ, as Campanula cervicaria, lamiifolia, glomerata, and pyramidalis, but not C. Medium or rapunculoides; further, those bundles, accompanied by milk-tubes, which are found in the same position in the Cynaraceous plant, Gundelia Tournefortii, and those which occur in many Cichoriaceæ of the genera Lactuca, Scorzonera, Sonchus, Tragopogon, Hieracium, but not in Chondrilla, Taraxacum, and Apargia. In Cichorium the bundles of sieve-tubes are absent in the stem, but appear in the petiole near to the vascular bundles[1].

In the cortical parenchyma outside the ring of vascular bundles sieve-tubes are of constant occurrence in thick Cucurbitaceous stems[2] (Cucurbita, Lagenaria, Cucumis, Ecbalium). Here they lie close to the inner limit of the intra-cortical ring

[1] Hanstein, Die Milchsaftgefässe, pp. 57, 68, &c.—Trécul, Comptes Rendus, 27 Nov. 1865.
[2] Sanio, Botan. Zeitg. 1864, p. 227.

of sclerenchyma, either singly or 2–3 together, running longitudinally through the internodes, and often anastomosing at the nodes with the sieve-tubes of the vascular bundles. Trécul describes small bundles of sieve-tubes, accompanied by laticiferous tubes, distributed in the peripheral cortex of Gundelia Tournefortii. Also the bundles described by Sanio, *l. c.*, in the cortex of Plantago and Trientalis perhaps belong to this category.

In many species of Potamogeton (P. natans, lucens, pectinatus) there is in many, but not all of the bundles of sclerenchymatous fibres which traverse the cortical parenchyma a small strand consisting of a few tubes, which is surrounded by the sclerenchyma as by a sheath (comp. Fig. 171). With the above may perhaps be grouped those bundles which can hardly contain sieve-tubes, found by Sanio [1] in the cortex of Elodea. Near to the Epidermis there are in the internode 6 bundles of some few (usually 5) thin-walled, elongated-prismatic cells, which alternate with the 6 rows of leaves. They run perpendicularly through the internode, and each gives off on each side at each node a horizontal branch, which anastomoses with the rudiment of a vascular bundle on its course into a leaf.

2. *Vascular bundles.*

Sect. 58. From the very first those bundles which consist essentially of definitely arranged groups of tracheæ and sieve-tubes, and which traverse the body of the plant as a continuous system, with blind endings only in the growing-points and at the ends of peripheral branches, have been called *Vascular bundles*, Fasciculi vasorum. Inasmuch as the vascular bundles are not unfrequently accompanied by sclerenchymatous fibres, the term *Fibro-vascular bundles* has in recent times been frequently applied to them [2].

The general arrangement of the tracheæ and sieve-tubes, which are united to form the bundles, is defined partly by their arrangement in the single bundle, partly by the arrangement or course of the bundles in the plant. The former, that is the structure of the single bundle, may, as is shown by experience, change in different parts of its course. A synoptical description of the structure of the individual bundles must therefore presuppose a knowledge of their course, and the general description must deal with this first.

A. ARRANGEMENT OF THE VASCULAR BUNDLES.

a. *Course of bundles in the root.*

Sect. 59. In the *individul root* a bundle which terminates at the growing-point, and which grows with it, runs almost exactly along the longitudinal axis; in Isoetes [3] it is strongly excentric, and nearer to that side of the root which is opposite the

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[1] Sanio, Botan. Zeitg. 1865, pp. 186, 191.

[2] Nägeli, Beitr. I.

[3] Compare Von Mohl, Linnæa, 1840; Verm. Schriften, p. 122, &c.—Hofmeister, Abhandl. d. K. Sächs, Gesellsch. d. Wissensch. IV. p. 147.

furrow of the stem. In the thick roots of the Pandaneæ and the genus of Palms, Iriartea, there are found a number of parallel bundles, which converge at the growing-point: as will be mentioned in Sect. 108, it may be doubted whether these should be called parts of one very large divided bundle, or so many individual bundles. The tuberous lateral roots of the Ophrydeæ, of Dioscorea Batatas, and of Sedum Telephium[1], are on the other hand traversed by numerous separate bundles which converge towards the apex, and are finally united into a short terminal portion. In the undivided tubers of Ophrydeæ they diverge from the point of insertion to the broadest transverse zone, and from thence towards the apex they curve and converge, and unite there into a single short apex, which ends blindly. During their course the bundles, especially the peripheral ones, are united here and there by anastomosing branches meeting the bundles at an acute angle. The lateral roots of the above species of Sedum, which require further investigation, appear to behave in a similar manner, but the anastomoses are absent, and the terminal point is more elongated. The thick cylindrical adventitious roots of Dioscorea Batatas, the development of which also requires further investigation, are traversed throughout their length by very numerous bundles: these are irregularly distributed over the whole transverse section, have a sinuous course, and are connected on all sides by anastomoses.

b. *Course of bundles in the individual leafy stem*[2].

Sect. 60. The bundles, which traverse the stem, are separable according to their course into two categories: firstly, such as always remain in the stem and grow acropetally with it: they may either have no direct connection with the bundles of the leaves, or the latter may be attached laterally to them: these are the *cauline* bundles, which belong only to the stem: secondly, the bundles *common to stem and leaf*, which run for a certain distance in the stem, and then enter a leaf, and thus belong in one part of their course to the stem, in another part to the leaf.

A stem may contain only cauline, or only common bundles, or both.

The direction of the course of the bundles follows generally the longitudinal axis of the stem: it is only in the nodes, and in some unimportant connecting branches, that the direction is exactly transverse. During this for the most part longitudinal course, their direction with relation to the plane of the surface, which may be provisionally considered as flat, and to that of a radial longitudinal section varies; a bundle may run perpendicularly or obliquely relatively to both; that is, it may be *radially-perpendicular* and *radially-oblique*, *tangentially-perpendicular* and *tangentially-oblique*. By combination of these conditions, curved, S-shaped, and spiral arrangements may result.

After traversing a certain distance, a bundle may connect itself with another to form a single one. There are accordingly distinguished *separate-* or *individual-*bundles, and *united* bundles.

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[1] Irmisch, Botan. Zeitg. 1855, p. 253.—Henry, Verhandl. Naturwiss. Vereins. f. Rheinl. und Westf. 1860.

[2] Von Mohl, Palmarum structura, Monachii, 1831.—Hanstein, in Pringsheim's Jahrb. I. p. 233.—Nägeli, Zeitschr. f. Wiss. Bot. Heft 3 and 4, p. 129.—Beitr. z. Wissensch. Bot. I.

Common bundles rise for a certain distance in acropetal direction through the stem, and then curve outwards at a node, to enter a leaf inserted at that point. Their course in the stem is most clearly understood by following them from their point of exit in a basipetal direction, that is, downwards. The description of their course in this direction also corresponds best to the facts, inasmuch as at least in most cases the development of the common bundles begins at the point of exit, and proceeds on the one hand towards the leaf, and on the other downwards in the stem.

From the point of exit in the node, the common bundle passes downwards through a number of internodes, and then affixes itself to, and unites with, another bundle, usually a common bundle, which makes its exit lower down. The junction is effected in most cases at or near a node.

The common bundles accordingly represent within the stem the anatomically demonstrable trace of the corresponding leaves: they are therefore called *bundles of the leaf-trace*, and the whole number of those which belong to one leaf form the trace, or internal trace of it[1].

The number of the bundles of a leaf-trace is constant, within narrow limits of variation, for each region of the stem of each species: but differs greatly according to the region and the species, varying from one to sometimes very high figures: the leaf-trace thus generally consists of one or many bundles.

A leaf-trace with many bundles may be distributed over a variable portion of the transverse section, or circumference of the stem, or, as Nägeli describes it, it may be of variable *width*. The latter may amount e.g. to $\frac{1}{10}$, $\frac{1}{2}$, $\frac{1}{1}$ of the circumference of the stem. Traces with one bundle, or narrow ones with more than one, become as a rule smaller, or narrower in a basipetal direction: wide traces with more than one bundle usually increase in width in the same direction, so that a lower one is enclosed by the one directly above it.

The number of the internodes, which a bundle of the trace, or a whole trace traverses before it reaches the point of junction, is constant within narrow limits of variation for each definite individual case, according to species and region: further, it is not less various in different individual cases than the above-named relations.

The individual bundle of a trace either remains undivided during its downward course, or it may be split into two or more shanks. The bundles of a multiple trace, as also of successive traces, may descend side by side, being thus *concomitant*; or they are separated from one another by other bundles, which pass between them, and *pectinate*[2] with them.

From the above it is plain that where bundles of a leaf-trace are present, a definite relation exists between the arrangement of the leaves at the periphery, and that of the bundles of the leaf-traces within the stem. If all bundles of leaf-traces were separate and concomitant, and had a perpendicular course, their arrangement in the transverse section of an internode would exactly correspond to the horizontal projection of the arrangement of those leaves, whose traces pass through

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[1] Hanstein, *l. c.*

[2] [Compare foot-note, p. 128.]

the internode[1]. This may be the case; but in most instances the direct relation between the two systems of arrangement is obscured and destroyed by oblique courses, pectinations, splittings, and coalescences.

The special phenomena of the distribution of bundles in the stem, which vary greatly, subject to the above general rules, may in some few cases be recognised as direct consequences of adaptation. For the most part they appear as anatomical characters (p. 25) of the groups of various rank distinguished in systematic botany, but vary individually within the groups of higher order, as freely as does the external conformation of individual species: their differences are often closely correlated with those of the latter, as might be expected *a priori*, but not uncommonly they show unexpected deviations.

In accordance with these facts as at present before us, the following synopsis of individual phenomena will best be arranged according to the main systematic divisions, while within these the arrangement will follow the phenomena of distribution of bundles. How far more general rules for individual families and genera or for certain categories of adaptation may be laid down within the main types first mentioned, will be in part obvious from the description of individual cases; while in other cases decision on this matter must be withheld till further investigations have been made, since in many families, especially of the Phanerogams, the course of the bundles has been investigated in single examples only, or even not at all.

I. Type of the Dicotyledons.

Sect. 61. By this name is indicated that course of the bundles which is characteristic of the stem of the very great majority of *Dicotyledons*: further, of those *Coniferæ* also which have been investigated, and of the *Gnetaceæ* with the exception of Welwitschia. Among the Monocotyledons many Dioscoreæ belong to this type, and of Filicineæ, the Equiseta and Osmundaceæ; these will however be treated in the later sections dealing with these orders.

All the primary bundles of this type are common bundles of the leaf-trace. They curve inwards into the stem at the node, and from thence they take a radially-perpendicular course down it, all of them remaining at about the same distance from the middle and from the surface of the stem. Leaf-traces with one bundle always pass down through more than one internode: this is also usually the case with those having several bundles. The insertion of the bundles on such as emerge from the stem lower down occurs as a rule at the nodes, or close to a node, and in such a way that they are connected in a unilateral-sympodial manner (Fig. 92), or in a reticulate manner by means of shanks or diverging limbs, which are attached to the neighbouring bundles on either side (e.g. Fig. 108).

From this course of the bundles results the characteristic, general, primary structure of the typical stem of the plants of this category. The bundles are arranged in the transverse section in a broken, ring-like series, the *ring* or *circle of vascular bundles*. The remaining, chiefly parenchymatous tissue in which they are imbedded, is separated into an axile, cylindrical or prismatic body, which fills

[1] Compare Karsten, Veget. Org. d. Palmen. Abhandl. d. Berlin. Acad. 1847, p. 208.

the ring—this is the *pith* or *Medulla*; a mantle, covered by the epidermis, and surrounding the ring externally—this is the *outer cortex*; and the bands which lie between the bundles, and pass radially, as seen in transverse section, from the cortex to the pith—these are the primary connections with the pith, or *primary medullary rays*. The form and number of the latter is defined in each individual case, in the first instance, by the above-mentioned general rules for the number of bundles, and for the course of the leaf-traces: their form depends upon the relative width of the vascular bundles.

In the following paragraphs will be given the most important known individual cases, following in the main the fundamental investigations of Nägeli, while the most prominent general rules will be more thoroughly exemplified by some few instances.

A. Dicotyledons.

I. **Hypocotyledonary stem.** In most species investigated two bundles of the trace enter the hypocotyledonary stem from each cotyledon: these usually unite at the base of the cotyledon as its central nerve (*e.g.* Plantago, Urtica, Mercurialis, Antirrhinum, Impatiens, Tropæolum, Vitis, Lupinus, Lathyrus, &c.[1]). In Phaseolus the two bundles are sometimes separated, sometimes united. In many plants the trace of the cotyledons consists of but one bundle (*e.g.* Papaver orientale, Lepidium sativum, Spergula arvensis, Silene[2], Portulaca oleracea, &c.), though it is possible that here also this often arises through the very early coalescence of two bundles. In Cucumis sativus and Melo 4, and in Mirabilis Jalapa 5 bundles enter the cotyledons, in Ricinus communis 4 or 5. From the cotyledonary node the bundles run vertically downwards, and unite at the base of the hypocotyledonary part. Where the trace of the cotyledons is a single bundle these remain throughout separate and undivided. Where it consists of two bundles their behaviour is not uniform. Either the two bundles of one trace approach one another, and finally unite as a single bundle; or the non-equivalent bundles of the two traces unite, the right-hand bundle of the one with the left-hand bundle of the other. A transverse section shows in the first case two bundles, the position of which corresponds to that of the cotyledons (Lupinus luteus, Lathyrus Aphaca, Urtica Dodartii); in the second case two bundles alternating with the cotyledons (*e.g.* Antirrhinum majus, Tropæolum majus, Impatiens Balsamina, Vitis vinifera). The four-bundled traces of the cotyledons in Cucumis are united at their margin, since the lateral bundles from the respective cotyledons coalesce with one another—thus the transverse section of the hypocotyledonary stem shows 6 bundles, 4 separate and 2 united: the two latter separate again at the base into two shanks, and unite with the first four. The 8, 9, or 10 bundles, which enter the cotyledons, unite in Ricinus to 4, in Mirabilis to 2.

The bundles, which enter from the leaves next above, insert themselves in the cotyledonary node on those of the cotyledons, or run down into the hypocotyledonary stem, and finally unite with them there: the latter is the case *e.g.* in Lupinus and Phaseolus (see below under 4).

II. **Region of Foliage.**

1. *Leaves arranged spirally, leaf-trace a single bundle.* 'The bundles from the leaves descend through many internodes, and usually unite with those of definite lower leaves, so that a transverse section shows the traces in a definite spiral series, which is not identical with the spiral of the leaves, but is related to it.'

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[1] Nägeli, *l.c.* p. 61.—Lestiboudois, Phyllotaxie anatomique, Ann. Sci. Nat. 3 sér. tom. X. p. 19.

[2] Rohrbach, Monogr. d. Gattung Silene, p. 22.

Iberis amara (Figs. 92, 93), foliage shoot. The arrangement of leaves in the terminal bud is $\frac{5}{13}$. Each bundle descends through 10 or 11, rarely 12, internodes and inserts itself there on that of the 5th lower leaf. Meanwhile it describes the form of an elongated S, since it bends from the vertical, first to the ascending or anodic side of the leaf-spiral, then to the descending or kathodic side in a tangential direction. The bundles thus run separately through 5, 6, or 7 internodes. By their coalescence there are formed 5 sympodial bundles, which traverse the whole stem: these complete a circuit in 65 internodes, while the separate bundles appear as one-sided branches from them. The oblique course of the leaf-traces is contrary in direction to the leaf-spiral; *i.e.* if the latter were right-handed, the bundles would curve upwards towards the left. Oblique connecting bundles appear later between the leaf-traces, originating in the 14–18th internode which has vascular bundles.

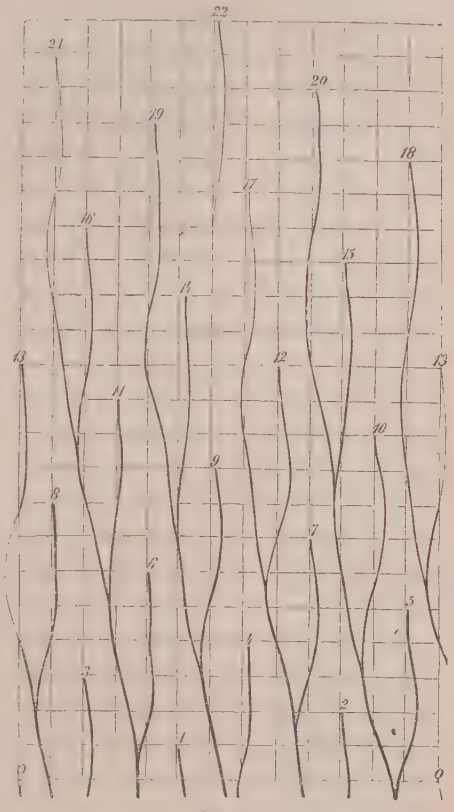

Fig. 92.

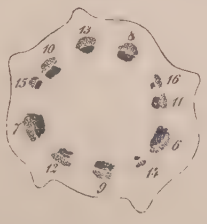

Fig. 93.

FIGS. 92, 93.—Iberis amara, after Nägeli. Fig. 92. Scheme of the course of the bundles in the young foliage shoot; the ring of bundles spread out in a vertical plane. The figures indicate the successive bundles of the leaf-trace at their point of exit from the ring into the leaf. —Fig. 93 (15). Transverse section through the internode above the point of exit of bundle 5; meaning of figures as in Fig 92.

To this type belong further *Arabis albida*, *Jasminum fruticans*, *Sarothamnus scoparius* (comp. Nägeli, Hanstein, *l.c.*).

2. *Leaves spirally arranged. Leaf-trace of more than one bundle, pectinating at most with the fifth trace below.* Several (3 or 5) bundles go from one leaf through the stem, and unite sooner or later with one another. These pectinate with the trace of the fifth or a still lower leaf.

Lepidium sativum. The cotyledons and the two succeeding almost opposite primordial leaves have traces with a single bundle. Of the later leaves, which are all arranged spirally, some few of the first have 3 bundles, one strong median bundle, and two weaker later ones, which unite immediately on entering the stem. In all the later leaves the median bundle is divided into 3. At the point of transition from stem to leaf 5 bundles are seen, of which the median ones are formed first, the two marginal ones last. The 3 median bundles are rather stronger, and unite above to form the median bundle of the leaf. Below, they separate from one another, and the 2 weaker marginal bundles unite with them, so that the leaf-trace now descends through the stem as three

bundles. Sometimes only one marginal bundle unites with the median, sometimes neither. These 3, 4 or 5 bundles of a trace rarely run unaltered through the stem: the appearance of a trace is varied by occasional splittings and reunions, so that it may retain 3–5 bundles (with a width of $\frac{1}{8}$th to $\frac{1}{3}$th of the circumference of the stem), or be reduced to 2 or 1 bundle. The leaf-trace may be followed through 6–8 internodes, but further down it is impossible to recognise with certainty how many bundles belong to each leaf. Within the first 5 internodes no crossing or uniting with lower leaf-traces has been observed. To this type belong *Impatiens Balsamina* and *Scopolina atropoides* (Nägeli).

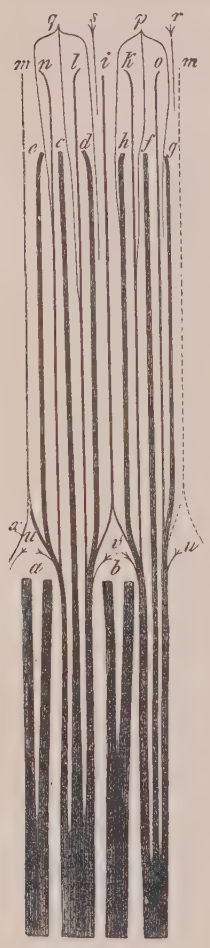

Fig. 94.

Fig. 95.

FIGS. 94, 95. — Lupinus Lehmanni, after Nägeli. Fig. 94, Scheme of the course of bundles of a seedling, the cylindrical surface being exposed in one plane; seen from within. — Fig. 95 (10). Transverse section through the stem above the cotyledons. The letters the same in both figures.

3. Leaves spirally arranged. Leaf-trace of five bundles, pectinating with the third or fifth. *Cocculus laurifolius* (Nägeli).

4. Leaves spirally arranged. Leaf-trace of three bundles which pectinate with the second and third.

Lupinus Lehmanni, Hort, and *L. luteus*, L. (Figs. 94, 95). In the seedling a pair of opposite primordial leaves, or first foliage leaves alternates with the two cotyledons. The second pair of foliage leaves, of which one is inserted rather lower and develops earlier than the other, alternate with the above, and are thus opposite the cotyledons. The two leaves of the third pair are not only at an unequal height, but also show a distinct horizontal deviation from the opposite arrangement. The fourth pair is intermediate between an opposite and spiral arrangement; all later leaves are arranged in a spiral.

Each cotyledon has a leaf-trace of two bundles (*a*, *b*), which become united into one in the lower portion of the hypocotyledonary stem. Sometimes there is found a third weaker bundle between the two bundles of one cotyledon. All later leaves have three bundles. Those of the primordial leaves, which will be called III and IV (*c*, *d*, *e*, *f*, *g*, *h*), are concomitant with the cotyledonary traces, so that a transverse section in the upper portion of the hypocotyledonary part shows 10 bundles, two being opposite two, and three opposite three. The median bundles (*i*, *m*) of the second pair of leaves (leaves V, VI) pass downwards through two internodes: on arriving at a median point above the trace of the cotyledons they curve, the one to the left the other to the right, and converging with the lateral bundles of trace No. III, they immediately insert themselves upon them. Later a second rather weaker shank (*v*, *x*) is formed on each: this curves, above the trace of the cotyledon, to the opposite side, and is inserted on the opposite lateral bundle of leaf No. IV. The lateral bundles of the pair of leaves V and VI (*l k*, *o n*) descend through one internode, and cross the lateral bundles from III and IV at the next node; in the following internode they lie at the inner side of these, and are inserted upon them at the cotyledonary node, or rather lower.

The median bundles (*p*, *q*) of the third pair of leaves, VII and VIII, pass through two internodes, and pectinate there with the traces from III and IV: *p* lies between the median and the ascending, or anodic lateral bundle from IV, *q* between the median and descending, or kathodic lateral bundle from III. They are inserted on the above lateral bundles in the third internode. The median bundle from leaf No. IX (*r*) applies itself to the ascending side of that of leaf No. VI (*m*), that from leaf No. X (*s*) to the ascending side of that of leaf No. V (*i*).

u and *v* above *a* and *b* are bundles entering from the axillary buds of the cotyledons, which apply themselves to the lateral bundles from III and IV.

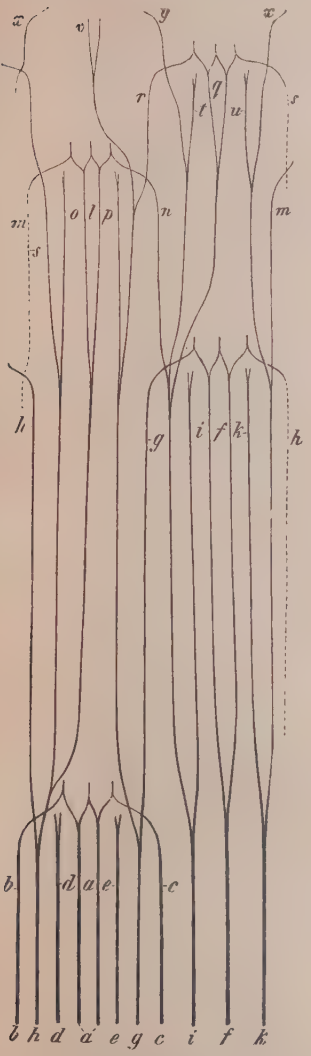

Fig. 96.

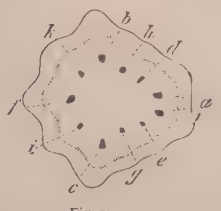

Fig 97.

FIGS. 96, 97.—Aristolochia Clematitis, after Nägeli. Fig. 96. Scheme of the course of the bundles in the stem; the cylindrical surface reduced to one plane, and seen from within.—Fig 97 (20). Transverse section through an internode, at the height of the lower end of Fig 96; further explanation in the text.

To this type belong also *Erythrina crista galli*, *Prunus avium*, *Ribes rubrum*, *Menispermum dauricum*.

5. Leaves arranged spirally. Leaf-trace of 3 bundles, pectinating with the 1st and 2nd below.

Passiflora Vespertilio, *Viola elatior*, *Tropæolum majus*, *Cucumis sativus*.

6. Leaves spirally arranged. Leaf-trace of 7 bundles, all the bundles pectinating with those of the next trace. *Saururus cernuus*.

7. Leaves arranged spirally. Leaf-trace of 8 bundles, the lateral ones united. *Liriodendron tulipifera*, L.

8. *Leaves alternating in two rows.* Leaf-trace of 3 bundles, pectinating only with the leaf-traces of the same side. *Hertia crassifolia*, Näg. *l.c.*

9. Leaves alternating in two rows. Leaf-trace of 3 bundles, which pectinate with the traces of both rows: foliage shoots of *Aristolochia Clematitis*, A. *Gigas*, *Sipho*. (Nägeli, *l.c.*).

In A. Clematitis (Figs. 96, 97) three bundles enter the stem from the leaf. The median bundle divides immediately into two, which traverse the first internode side by side, and, uniting again with one another at the next node, they pursue a common course through the next internode. The two lateral ones pass undivided through two internodes: at the point of exit into the base of the leaf they are united with the two shanks of the median bundle by an anastomosis. Side by side with the two shanks of the median bundle lie, on the right and left-hand, bundles which pass out at the same node, and supply the axillary inflorescence: they are therefore axillary bundles. The whole trace of the lateral structure of a node thus consists in its own internode of 6, in the next lower internode of 5 bundles. It encloses in the former an arc of 215°, in the latter of 205°.

The median bundle of the trace (*a*, *f*, *l*, *q*, *v*) as it reaches the four bundles of the leaf-trace of the second node curves to one side, and unites with the lateral bundle of the next lower trace. The median bundles of a row of leaves curve alternately to both sides, *e.g.* those of the traces 1, 5, 9 to the right, those of 3, 7, 11 to the left. At the point of curvature a second shank is formed later, which affixes itself to the other lateral bundle.

The lateral bundles of the leaf-trace (*bc*, *gh*, *mn*, *rs*, *xy*) pursue an individual course through their own internode, they then pectinate with the corresponding ones of the next

lower node, they traverse the next internode in conjunction with the median bundle of the next upper leaf, and each inserts itself in the second node on an axillary bundle of the next lower trace. The two axillary bundles, *dc*, *ik*, *op*, *tu*, take an independent course in their own internode, in the next they combine with the lateral leaf-bundles of the next higher trace, and insert themselves in the second node on the lateral leaf-bundles of the next lower trace. These conditions are very regular: the transverse section through an internode therefore shows regularly 11 bundles; Fig. 97 shows the arrangement of these, and explains them by means of the same lettering as at the lower end of Fig. 96.

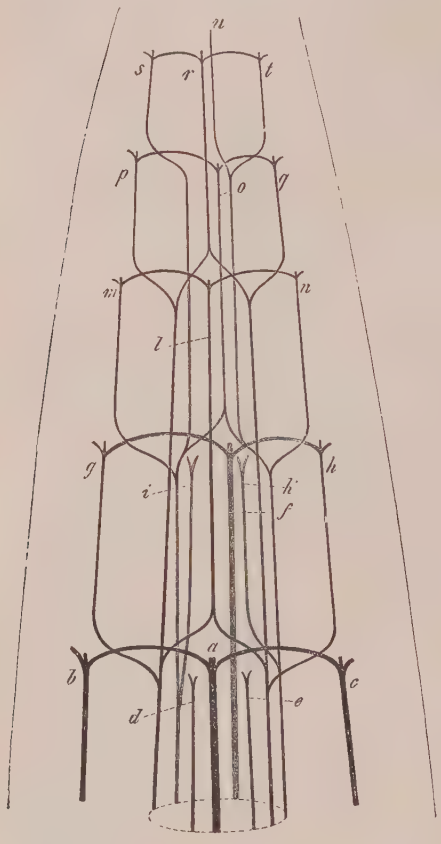

Fig. 98.

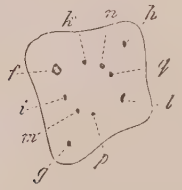

Fig. 99.

FIGS. 98, 99.—Lathyrus Pseudaphaca, after Nägeli. Fig. 98 Scheme of the course of the bundles in the apex of the stem supposed to be transparent; the bundles on the side further from the observer are paler, those on the near side are black.—Fig. 99 (25). Transverse section through an internode such as the lowest but one of Fig. 98; with the same lettering as the latter.

10. Leaves alternating in two rows. The rows are nearer one side in the terminal bud. Leaf-trace of 3 bundles, which pectinate with the traces of both rows.

Medicago sativa, *Lathyrus Nissolia*, *L. Aphaca and Pseudaphaca*, *L. Odoratus*, *L. purpureus*.

L. Aphaca and Pseudaphaca (Figs. 98, 99). The leafy stems are four-cornered, the corners are sometimes slightly extended as wings. The transverse section (Fig. 99) shows in each of the two opposite lateral edges a bundle (*h*, *g*) and internally a circle of 8 and more bundles, which later decrease in number by coalescence. The median bundle of the leaf-trace divides as it emerges into the leaf into 3 branches, of which the central weaker branch enters the petiole, while the lateral ones form bow-like anastomoses with the two lateral bundles: from these arise the bundles for the stipules.

The median bundle (*a*, *f*, *l*, *o*; *r*, *u*) runs separately down through two internodes, then curves to one side (*u*), and later it forks into two shanks. These insert themselves on the lateral bundles of the next lower leaf-trace. The two lateral bundles (*bc*, *gh*, *mn*, *pq*, *st*) run first in the corners through their own internode: at the next node they enter the circle of bundles of the trace, where they pectinate with the lateral bundle of the next lower trace: each then unites with one shank of the median bundle of the next higher trace, and running together with it through two internodes, inserts itself finally in the third internode below on the lateral bundle of the second lower trace.

If a peduncle is seated in the axil of the leaf it receives two bundles from the stem (*de*, *ik*), which usually run separately through one internode, and affix themselves in the next node to the lateral bundles of the next higher trace. In this case the transverse section (Fig. 99) shows eight bundles, or, when the axillary bundles are absent, six bundles arranged in a circle, and with two more in the corners. Variations from this type are brought about by the bundles uniting higher or lower, and by variations of the pectinations. The width of the leaf-trace in the first two internodes is 190° to 210°.

11. Leaves alternate, in two rows. Leaf-trace usually of five bundles, the lateral

Fig. 100.

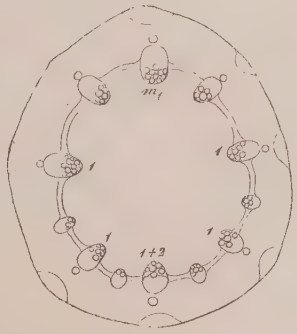

Fig. 101.

FIGS. 100, 101.—Fœniculum officinale. Fig. 100. Scheme of the vascular system for leaves with seven bundles, the cylindrical surface being reduced to a single plane; at the level of the figures 1, 2, 3 are the nodes. *m* always indicates the median bundle passing out at the node; *l* the marginal bundles.—Fig. 101 (40). Transverse section through an internode with arrangement and number of bundles corresponding to that of Fig. 100. 1. The bundles of the trace from the next higher leaf, m_1 its median bundle; 1+2 the bundle formed from the marginal bundles of 1 and the median bundle of the leaf next but one above. The bundles alternating with those numbered are the united traces of the two leaves above 1; between the bundles is indicated the cambium zone which connects them. The small circles outside the stronger bundles are the transverse sections of oil passages; in each of the blunt angles of the stem is the transverse section of a bundle of fibres having the shape of a segment of a circle.

bundles of two successive leaves are not completely pectinated. *Vitis vinifera*, *Ampelopsis hederacea*.

12. Leaves alternate, in two rows. Leaf-trace usually of five bundles, the lateral bundles of two successive leaves completely pectinated.

Phaseolus vulgaris, *Ph. multiflorus*—Nägeli, *l. c.*; Dodel. in Jahrb. f. wiss. Bot. Bd. VIII.

13. Leaves alternate, in two rows. Rows approaching one another on one side. Leaf-trace of 7–9 bundles. All bundles of two successive leaves pectinated. *Platanus occidentalis.*

14. Leaves alternate, in two or more rows. Leaf-trace of numerous bundles. All bundles of two successive leaves pectinated. To this type belongs *Menyanthes trifoliata*, with leaves in two rows, and a trace consisting of 10–13 bundles, according to Nägeli: also many Umbelliferæ.

According to investigations[1] on Æthusa Cynapium, Phellandrium aquaticum, Hydrocotyle vulgaris, and Fœniculum officinale, the Umbelliferæ of the usual form have in the non-flowering shoots a bundle system, which in accordance with their similarity in external conformation is similar in its main features, though it shows individual variations. The following scheme may be constructed for it (comp. Figs. 100, 101). The leaves are in two alternating rows, or spirally arranged: their base completely encircles the stem, one margin even overlapping the other; each leaf-trace has several bundles, its width being equal to the whole circumference of the stem ($\frac{1}{1}$); the leaf-trace, pectinating with those of the next higher and next lower leaves, and passing downwards through two internodes, inserts itself in the third node on the trace which comes down from the second node, and takes up in the second node the trace which emerges next above it. Each bundle of the trace runs directly downwards from the node (3), in which it emerges, through its internode; it takes up in the next node (2) a bundle of the trace which comes from above (3), and which affixes itself upon it; it passes in (2) between two bundles, which here enter the leaf, and runs between these down to the node (1). Here turning either right or left it affixes itself to one, or branching, to two neighbouring bundles, which descend from node (2). Whether the junction be to the right or left, or branched and on both sides, seems to be often subject to variation. Not unfrequently the branching arises later by the subsequent appearance of a second shank on a bundle originally attached on one side. If the bundles of successive traces are of equal number, and their number $= n$, the transverse section of an internode shows $2n$ bundles of the trace, and of these n are stronger and go to the next leaf, n are weaker, alternate with the former, and enter the second leaf above.

In the three-bundled traces of the creeping foliage-shoots of Hydrocotyle vulgaris no variation from this type was observed. In other cases, with a larger number of bundles of the trace, variations are frequent. They depend sometimes on inequalities in the number of bundles in the successive traces, since as the strength of a shoot increases the number of bundles of the successive traces enlarges, and then two or three bundles may pass between two bundles of the next lower trace: sometimes on the fact that the width of a trace (and leaf-insertion) is less than $\frac{1}{1}$ of the circumference of the stem, in which case certain bundles pass down through more than two internodes: sometimes there occur variations independently of these, in the same species, and possibly even in one and the same shoot, while many species have constant specific peculiarities. Thus the young plant of Fœniculum officinale (Fig. 100) has alternating leaves in two rows, their median planes diverging by 180°: the width of the leaf-insertion is $\frac{1}{1}$ or $> \frac{1}{1}$ of the circumference of the stem, that of the leaf-trace $\frac{1}{1}$. The number p of the bundles entering one leaf is, as in other investigated species, an uneven number: 5, 7, to 21 and more. Of the p bundles of one leaf the two marginal ones, *l. l.* Fig. 100, converge as they enter the node (1), and unite there at once with the median bundle (*m*) of the next higher leaf, which descends perpendicularly between them. This united bundle then descends further perpendicularly through the next internode, and forks in the next node (2), close above the median bundle, which passes out at that point, and each of its two shanks unites with the bundle, which descends side by side with it. The course of all other bundles corresponds to the scheme. The number n of the bundles of one leaf-trace in an internode is thus in Fœniculum $= p - 1$, while in cases which follow the scheme

[1] Carried out in 1873, in the Botanical Institute at Strassburg, by Herr von Kamienski.

exactly it is = *p*. The transverse section of the internode of Hydrocotyle shows, e.g. six alternating unequal bundles, if three enter each leaf: that of Fœniculum shows, when the number from each trace is equal, twelve (Fig. 101) if seven enter each leaf, and sixteen if nine bundles enter each leaf. As the result of inequality in number of successive traces in the growing plant, there occur also in Fœniculum deviations from the above special scheme. Those modifications of the course of the bundles, which certainly occur in the flowering shoots of the Umbelliferæ in question, and in many with deviating conformation, have not been investigated.

15. *Leaves opposite*, the pairs decussating more or less exactly. The bundles of one pair pass perpendicularly down through two internodes, and then curve, in the second lower node, sometimes converging symmetrically, sometimes both turning in the same direction, and then descend further, and unite with those belonging to lower leaves. This condition is plainly seen in the youngest stages only, later a second shank is usually formed at the point of curvature, so that the bundle becomes branched, and sits astride of that directly below it (Fig. 102). Further in many allied cases, the lower ending of the bundles becomes quite indistinct, by their coalescing laterally by means of intermediate bundles which appear very early (Chap. XIV).

To this category belong, according to Nägeli and Rohrbach (*l. c.*), *Fraxinus excelsior*, *Vinca minor*, *Apocynum hypericifolium*, species of *Phlox*, *Veronica incisa*, *Calluna vulgaris*, *Hypericum quadrangulum*, *Androsæmum*, *Euonymus europæus*, species of *Alsine*, *Spergula*, *Cerastium*, *Dianthus* and *Silene*, also *Galium* and *Rubia*. Figs. 102 and 103 may illustrate the arrangement for the special case of Cerastium. Fig. 102 is the scheme for the course of the bundles of a shoot with the cylindrical surface reduced to one plane; *ab*, *cd*, *ef*, *gh*, are the bundles of foliage leaves, the letters standing at their point of exit from the ring. Below the node marked *dc* these bundles of the trace are alone present. Above *dc* there are also others, viz. *p*, *o*, *n*, the bundles of the terminal flower-stalk, and *hi*, *lm*, of which pairs one enters each of the branches in the axils of the leaves *g* and *k* (comp. Sect. 94). All these bundles have a place in the ring as shown in Fig. 103, which represents a transverse section through the internode above *ef*.

Fig. 102.

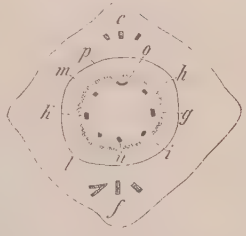

Fig. 103.

FIGS. 102 and 103.—Cerastium frigidum, after Nägeli. Fig 102. Scheme of bundle-arrangement; explanation in the text.—Fig. 103 (20). Transverse section through a shoot in the internode above *e*, *f* of Fig. 102. The letters indicate the same bundles in both figures; *e*, *f* are already branched in Fig. 103, in the sheath-like connate bases of their pair of leaves.

16. Leaves in whorls: traces consisting of one bundle, which runs down more than two internodes. *Trevirania longifolia*, *Russelia juncea*.

17. Leaves opposite: traces of three or four bundles, which unite at the second lower node with those of the next lower pair: not pectinated. *Antirrhinum majus*, *Ruellia maculata*, *Bignonia serratifolia*, *Tecoma radicans*.

18. Leaves opposite and decussate. Traces of 2 bundles, not pectinated. *Anagallis arvensis*, *Stachys angustifolia*, *Satureja variegata* Hort. (Nägeli, *l. c.*), and many other Labiatæ, *Nepeta Cataria*, *Melissa officinalis*, &c. Two bundles, which are united in the petiole to form one, separate from one another at once in the stem of the Labiatæ (Figs. 104 and 105),

and pass down the corners, between which the leaf is placed, through two internodes. At the second lower node they unite with those of the next lower trace, after having traversed one internode close side by side with these. The transverse section below the apex of the stem thus always shows eight bundles, in groups of two beneath the corners; those of each pair are of unequal size, the stronger belonging to the leaf-trace of the nearer pair of leaves, the weaker to that of the next pair. The bundles of one corner soon unite, as vessels appear between them. The transverse section then shows four bundles, which later unite to form a closed ring (Chap. XIV).

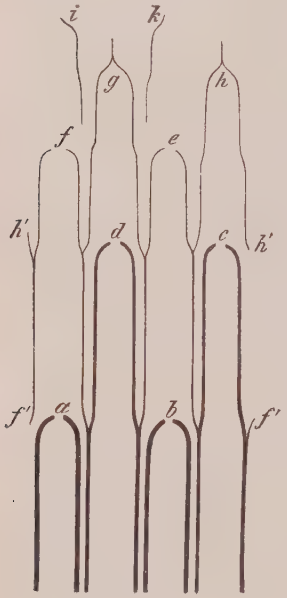

Fig. 104.

Fig. 105.

FIGS. 104 and 105.—Stachys angustifolia, after Nägeli. Fig. 104. Scheme of the vascular system in the end of the shoot, the cylindrical surface being exposed in one plane. *ab*, *dc*, *fe*, *gh*, *ik*, the traces of successive pairs of leaves, the letters being placed at the nodes; from the highest pair only one bundle of each trace is as yet visible, *ik*.—Fig. 105 (35). Transverse section through a young internode, corresponding to that above *a b* in the above figure; the same bundles are indicated by the same letters as in the above.

19. Leaves opposite, traces of 3 bundles: the lateral bundles pectinating with those of the next pair.

Clematis Vitalba, *Viticella*; *Atragene*, *Urtica Dodartii*, *Lonicera* spec., *Acer pseudoplatanus*, *Philadelphus coronarius*, *Tagetes lucida*, *T. signata* Bartl., *Humulus Lupulus*, *Centranthus ruber*, *Æsculus macrostachya*, *Euphorbia Lathyris*.

The foliage shoots of the above plants, though corresponding in the above points, differ in the unequal length of the course of the traces. The median bundles sometimes insert themselves at the next lower node, sometimes at the next but one, sometimes still lower. The lateral bundles also pass through one, two, or several sections of the stem. Giving the reference to Nägeli's work, we will here describe only the very simple examples of Clematis and Atragene (Figs. 106, 107).

The pairs of leaves decussate at right angles. The six corners of the internodes, of which two opposite ones corresponding to the median points of the leaves are rather more prominent, alternate regularly. The width of the three-bundled leaf-trace is about 115°.

The median bundles (*ad*, *gk*, *qn*, *xt*) pass through one internode, divide at the next node into two shanks, and insert themselves with these on the lateral bundles of the pair of leaves at that point. At first there is always but one shank present, and the two median bundles of the same pair have (according to two observations) a symmetrically converging curvature. The formation of the second shank often appears at a late stage in Cl. Viticella, or is entirely absent.

The two lateral bundles of the leaf (*bc*, *ef*, *hi*, *lm*, &c.) also pass through one internode, they curve in a converging manner at the next node, and insert themselves on those same lateral bundles, with which the shanks of the median bundle unite. In Cl. Viticella the leaf-trace in this condition is usually complete: in Cl. Vitalba a second shank is formed at the point of curvature of the lateral bundles also: this curves to the opposite side, and coalesces with a median bundle of the node. The transverse section of the young internode shows six bundles of the leaf-trace (Fig. 107, p. 246).

The axillary branches have also six bundles in their lowest internode, which unite to two on entering the stem. These two unite at once right and left with the median bundle of the leaf which bears them.

20. Leaves opposite: traces consisting of three bundles, the lateral bundles of the same pair united from the first. *Mercurialis annua* and *M. perennis*.

21. Leaves opposite: traces consisting of five bundles, the two lateral bundles of the same pair united from the first. *Sambucus nigra*.

B. Gymnosperms[1].

As has been above mentioned, the vascular system in the stems of the Coniferæ does not differ from that of the Dicotyledons: they will therefore be mentioned here only as special instances of the type of the Dicotyledons.

The seedling of most of them has two opposite cotyledons which grow green on germination, and rise above the ground; rarely (Ginkgo, Araucaria, section Columbea) they remain in the ground. More than two occur exceptionally in many genera, and constantly in Taxodium (4 to 9) and in the Abietineæ, in the sense of Strasburger, i. e. Linnæus' genus Pinus. The number of the cotyledons differs here according to the species, and varies in the same species within wide limits: e. g. in Abies pectinata between 4 and 7, in Pinus sylvestris between 3 and 8, in Pinus Pinea between 8 and 14. Discounting single exceptions to be named below, one bundle enters the short hypocotyledonary section from each cotyledon; where there are two cotyledons both bundles run vertically downwards, and soon undergo coalescence to form the root-bundle: where the number is higher, two or three bundles coalesce immediately after entering the hypocotyledonary section to form one, so that the number of the bundles of the trace in the latter is smaller than that of the cotyledons. Statements by Lestiboudois (*l.c.*, pp. 25 and 26) lead to the assumption that in Cupressus pyramidalis and Abies balsamea the bundle, which passes from the cotyledon into the stem as a simple bundle, splits at the node into two shanks, and that the opposite shanks of two neighbouring bundles unite into one, which (alternating with each pair of cotyledons) descends perpendicularly. The cotyledons of Araucaria brasiliensis[2] have each 8 vascular bundles, and these each unite in the cotyledonary node to two, so

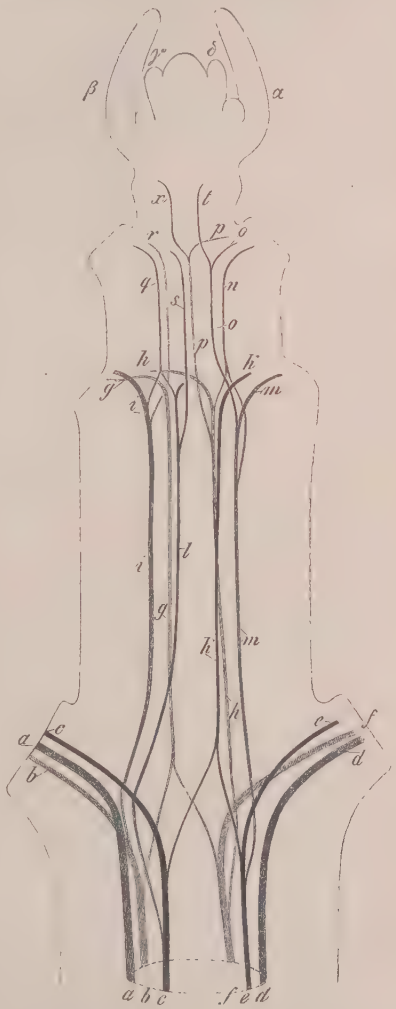

FIG. 106 (40).—Clematis Viticella, after Nägeli. End of a branch made transparent by removing the surface and treatment with potash, showing the course of the leaf-traces. The outgoing ends of the bundles are somewhat distorted by slight pressure; the two highest pair of leaves α β and γ δ have as yet no developed bundles.

[1] Nägeli, *l.c.*—Lestiboudois, *l.c.*—A. B. Frank, Botan. Zeitg. 1864, p. 150.—Geyler, Gefässbündelverlauf in d. Laubblattregion d. Coniferen, Pringsheim's Jahrb. VI.—Strasburger, Die Coniferen und Gnetaceen.

[2] Strasburger, *l.c.* p. 369.

that from the two cotyledons four bundles of the trace pass down into the hypocotyledonary section.

In all investigated cases the bundles of the trace of the first epicotyledonary leaves insert themselves on the cotyledonary bundles at or close below the cotyledonary node.

With the single exception of Ginkgo, the trace of foliage and scale leaves passing through the stem is in the Coniferæ a single bundle; and this is still the case even where the leaves have several bundles, and where these arise, as in Dammara and the broad-leaved Araucarias, by splitting of the single bundle of the trace while still in the node.

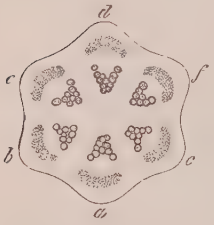

FIG. 107 (20).—Clematis Viticella. Transverse section through a young internode; further explanation in the text.

In the investigated species of Juniperus, Frenela, Cupressus, Callitris, Libocedrus, Thuja gigantea Nutt, Chamæcyparis ericoides Hort., the leaves are arranged in two- or many-membered alternating whorls. Their traces consisting of a single bundle descend undivided through one internode, and fork about the middle of the second internode into two shanks, which insert themselves right and left upon the bundles of the trace of this internode (Fig. 108).

Thuja occidentalis, Th. plicata, and Biota orientalis have on the other hand, it is true, the same whorls of two alternating leaves as their nearest allies above named; but the opposite traces of each pair of leaves pass perpendicularly downwards through two internodes without dividing; they then curve over the leaf-trace, which emerges at the 2nd lower node, both turning in the same direction (more rarely converging symmetrically), and affix themselves laterally on the bundles which emerge at the 2nd, 3rd, or rarely the 4th lower node (Fig. 109).

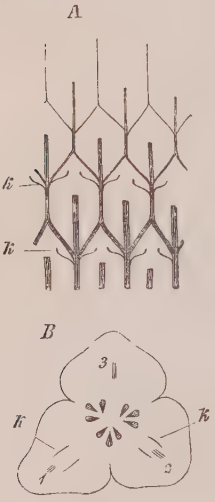

FIG. 108.—Juniperus nana, after Geyler. *A* scheme of the longitudinal course of the bundles, the cylindrical surface being reduced to one plane; the whorls of three members are slightly displaced spirally; *k* = bundles of the buds. *B* (16) transverse section through a young shoot; 1, 2, 3, the bundles, which pass out in the order of the figures to a whorl; *k* the bundles which pass into the axillary buds.

In the numerous Coniferæ with spirally arranged leaves, Chamæcyparis glauca Hort., Widdringtonia juniperina, the investigated species of Taxodium, Glyptostrobus, Cryptomeria, Sequoia, Cunninghamia, Pinus in the sense of Linnæus, Podocarpus, Saxegothea, Taxus, and Araucaria, the one-bundled leaf-traces have a course corresponding in its main points to the scheme described for Iberis (Fig. 110). Each bundle descends independently through a definite number of internodes, and then curving towards a definite lower bundle, affixes itself laterally on it, and coalesces with it further down. The number of the definite lower bundle, on which it is affixed, varies according to the individual case, but is constant for each single case, and follows the series 2, 3, 5, 8, 13, 21, ... The direction in which the apposition on the coalescing bundle takes place, is also constant for each individual case, and is defined by the number of the coalescing bundle, so that the apposition on the 3rd, 8th, or 21st lower bundle is in a descending direction, that on the 5th, 13th, or 34th in an ascending direction with reference to the leaf-spiral (Geyler, *l. c.*). The same rule above described is followed as regards the course of the bundles of the trace in the leaves of Cephalotaxus Fortunei, Torreya grandis, and, as far as at present known, of Dammara australis: these leaves appear at first in whorls, but are subsequently displaced spirally. Ginkgo also belongs to this category, since the two bundles of the trace, after running separately through 1–3 internodes, unite to one, which curves in a kathodic direction above the 5th lower trace, and inserts itself in about the 8th lower internode in an anodic direction on the 5th lower trace, with which it pursues a united course in the 9–11 internode.

Among the *Gnetaceæ*, *Ephedra* vulgaris has in each of the two cotyledons two vascular

bundles, these enter the hypocotyledonary stem, which thus contains four bundles of the cotyledonary trace. The epicotyledonary section contains eight bundles, four opposite each cotyledon. In the cotyledonary node these eight bundles unite in pairs, each of which passes down between two cotyledonary bundles, and splits within the hypocotyledonary section into two shanks, which insert themselves on the next cotyledonary bundles. Below this point of union the four cotyledonary bundles unite to form the bundle of the root.

Each of the other leaves of Ephedra, which, as is well known, are scale-like, and are arranged in accurately alternating whorls of two, also contains two bundles. In E. vulgaris the two-bundled leaf-trace enters the ring of bundles at its own node (1); takes a perpen-

FIG. 109.—Thuja plicata, after Geyler. *A* scheme of the bundle system, the cylindrical surface being reduced to one plane. *B* (16) transverse section through a young shoot. *1*, *1* the bundles, which pass directly into a pair of leaves; outside each, below the surface, is a resin passage, *h*.

FIG. 110.—Pinus sylvestris, after Geyler. Scheme of the vascular system in the young shoot, the cylindrical surface being reduced to a single plane; leaves arranged 8/21, in a right-handed spiral. The figures indicate the successive bundles of the leaf-trace, which are represented as broad bands. Each pair of converging bundles (represented as thin lines), near the emerging bundles 0—9, goes to an axillary shoot. The traces unite in descending order, each with the eighth lower one.

dicular and parallel course downwards through two internodes, and inserts itself in the third node laterally on the trace which emerges at node 2, each bundle joining with that laterally next it. In the node there appears at an early stage a transverse girdle of tracheides, which unites the bundles. Strasburger states for Ephedra campylopoda, that between the two bundles of the trace of each leaf there runs a 'complementary bundle' which arises from the girdle of tracheides: this passes through one internode, from the node of the pair of leaves, to the next transverse girdle. In Ephedra altissima, according to the same author, the two bundles of the trace of a leaf take a separate course only in their own internode, and in the next are united to a single bundle. E. vulgaris has therefore eight bundles of the trace in the internode, of these two opposite pairs belong to the same pair of leaves: E. campylopoda has ten, E. altissima only six.

The species of *Gnetum* have on their foliage shoots decussating pairs of leaves, separated from one another by elongated internodes. Each leaf contains four or five bundles, according to the species[1]. According to some few investigations on Gn. Thoa the leaf-traces follow the above-described scheme for the Umbelliferæ. The ten-bundled trace of each pair of leaves passes down through two internodes, and unites in the second node with the

[1] Strasburger, *l.c.* p. 115.

trace of the next lower pair. The bundles of the trace of successive pairs all pectinate with one another. Besides this, other coalescences must occur at or below the node, since in the internodes investigated the transverse section showed only eighteen bundles instead of twenty as assumed according to the scheme, and as actually occurs in Gn. Gnemon.

On Welwitschia comp. Chap. XVI.

To avoid repetition, the *Cycadeæ* will also be described in the chapter cited.

II. Anomalous Dicotyledons.

Sect. 62. A not inconsiderable number of Dicotyledons, some Cycadeæ, and Welwitschia differ in their bundle-system from that which characterises their allies, in that the primary bundles are not arranged in a simple ring. Either they contain a ring of bundles arranged according to the usual type, while additional bundles are found either within these, that is in the pith, or outside them, that is in the outer cortex; or the bundles are arranged in several, often not sharply distinguished circles, or so arranged that they appear in transverse section irregularly scattered between other tissues, with the exception of the most peripheral bundles, which may be distinguished as a ring well marked off from the outer cortex.

These more or less remarkable exceptions to the main type either occur in quite isolated species in typically formed genera and families (e.g. Umbelliferæ), or in numerous species of otherwise typically formed genera (e.g. Begonia), or they are characteristic of certain genera, or small families (e.g. Nymphæaceæ, Calycanthaceæ, Podophyllum, Diphylleja), more rarely even of large families, as Piperaceæ and Melastomaceæ. But even in the latter, exceptions occur to that grouping of the bundles which holds for the majority of their allies.

The above phenomena are based either upon an oblique radial course of the *bundles of the leaf-trace*, or upon the appearance of *cauline* bundles besides the bundles of the trace which are arranged in the typical ring. Discounting the Nyctagineæ, which will be described below (Chap. XVI), many Amarantaceæ, &c. with medullary bundles, the following cases belong to this category.

a. *Medullary bundles.*

1. *All bundles belong to the leaf-trace:* some on entering the stem are arranged in the typical ring, and have a radially perpendicular course in it: others, passing further inwards, are therefore medullary, and are either scattered through the pith or arranged in rings. To this class belong most *Cucurbitaceæ*, species of *Amarantus* and *Euxolus*, *Phytolacca dioica*, the *Piperaceæ*, doubtless also the herbaceous *Berberideæ*, *Podophyllum*, *Diphylleja*, *Leontice;* further species of *Papaver Thalictrum*, and *Actæa.*

The bundles of the climbing *Cucurbitaceæ*[1] (Cucumis, Cucurbita, Bryonia, Tladiantha, Cyclanthera pedata) are arranged in two rings (Ecbalium elaterium, which has no tendrils, has only one circle of bundles): those of the outer ring are opposite the corners of the stem, and are of equal number with these, e. g. five in Cucumis sativus, Cucurbita, Tladiantha dubia, Cyclanthera pedata, seven in Bryonia dioica: those of the inner ring alternate

[1] Bernhardi, Beobacht. über Pflanzengefässe, p. 20.—Sanio, Botan. Zeitg. 1864, p. 227.—Nägeli, *l.c.* p. 77.

with those of the outer, so that their outer portion falls between the latter, but their number is not always the same as that of the outer series, one being left out (e.g. $\frac{1}{4}$ in the specimens at hand of Tladiantha).

The bundles of both rings are, as far as investigated, bundles of the trace, which pass downwards on the average through two internodes: it remains for further investigations to ascertain their course exactly, a matter which is made very difficult by the early appearance of irregular transverse anastomosing bundles in the nodes.

Of those *Amarantaceæ*, which have been investigated, some, namely species of Celosia, Gomphrena, Alternanthera, Frœlichia, and Achyranthes, have the primary ring of bundles, and pith cylinder (the latter without bundles), which are typical of the Dicotyledons. In Amarantus[1] caudatus, A. retroflexus, and Euxolus emarginatus A. Br. the numerous (e.g. 11) bundles, which are arranged in the base of the leaf in a curved series concave upwards, separate from one another in the node, taking however a steep downward course: some form a ring with certain bundles, which descend from above, others penetrate deeper into the pith. Thus there are formed within the ring of bundles several irregular medullary rings, in which the bundles belonging to individual leaves remain grouped together. The middle of the pith has no bundles. The median bundles of each leaf-trace appear to penetrate deepest into the pith. Lower down the bundles of one trace unite, after traversing several internodes separately. An accurate investigation of their course remains still to be made. Slender specimens of Euxolus lividus Moq. show similar, but simpler conditions.

Phytolacca dioica has (according to Nägeli, *l.c.* p. 118) three bundles of the trace for each leaf. The two lateral ones descend in a radially perpendicular direction in the stem between the pith and outer cortex; they split first into two, then into several shanks, and these together form the ring of bundles. The median bundle enters the pith, but hardly deeper than $\frac{1}{8}$ the radius of the pith, it there descends through 8–12 internodes, and then again unites with the ring. It describes a curve convex inwards, the strongest curvature of which is in its upper part: it reaches nearest to the middle of the pith in the 3rd and 4th internodes. The transverse section through a mature internode thus shows 8–12 bundles, which are free within the ring.

The course of the bundles, which in the aerial stem of *Podophyllum*, Diphylleja, and Leontice[2] are distributed in the transverse section throughout the pith, almost as in the Monocotyledons, and of those which, in *Papaver* orientale (often also in P. somniferum), in *Actæa* racemosa, Cimicifuga fœtida, and species of Thalictrum, form an irregular 2- or 3-seriate zone round the pith, requires further investigation: it can hardly be doubted that they belong to the leaf-trace.

Further investigation must show whether the medullary bundles, which occur in *Statice* or the *Plumbagineæ*[3], belong to this series: I found no such bundles in the species of Statice, Armeria, and Plumbago which I examined.

Since P. Moldenhawer and E. Meyer it has been known that in the internodes of all *Piperaceæ* which have been investigated, with the exception of Verhuellia, there are medullary bundles, usually arranged in a circle, within a ring of bundles, which in the woody species (Pipereæ) subsequently undergo secondary thickening. Rarely more than one inner circle is present, e.g. in Peperomia variegata sometimes 2, in P. incana and obtusifolia 3–4, in Piper geniculatum 2, in Artanthe cordifolia 4[4]. The number of the

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[1] Link, Grundlehren der Anatom. und Physiol. der Pflanzen, pp. 144, 148.—Unger, Dicotyledonenstamm, p. 108.

[2] C. H. Schultz, Vaisseaux du latex, &c., Mém. prés. Acad. d. Sciences, VII (1841).—Sanio, *l.c.* p. 230.

[3] Russow, Vergl. Unters. p. 153.—Schwendener, Mech. Princip. p. 143.

[4] P. Moldenhawer, Beitr. p. 5.—E. Meyer, De Houttaynia et Saurureis, p. 39.—Unger, Bau, &c. des Dicotyledonenstammes, p. 68, &c.—Karsten, Veget. Org. d. Palmen, *l.c.* p. 148.—C. de Candolle, Mémoire sur la famille des Pipéracées, Mém. Soc. phys. de Genève, Taf. XVIII. p. 2.—

bundles, both of the inner and outer circle, varies, at least in many species, in the successive internodes of the same shoot. They run perpendicularly down the individual internode. In most species transverse anastomosis in the node makes it difficult to follow their further course. Most recent authors have arrived at the result that the bundles are partly common, partly, and especially the inner ones, cauline: the inflorescence certainly contains cauline bundles. Karsten alone, in the year 1847, expressed another view for the Piperaceæ, according to which all the bundles are bundles of the leaf-trace: this view is confirmed and generalised by the more thorough investigations of Weiss. The latter can only be epitomised here, reference being given to the original work, since the latter only appeared after this book had begun to pass through the press.

Peperomia galioides shows the course most clearly. The leaves are arranged in whorls of five, each has a single bundle. The bundles enter the node in the outer circle, and pass down in it through one internode: they then curve inwards, and, forming the inner circle, pass down the second internode: in the node below the latter they insert themselves on the bundles of the next higher whorl, which here curve into the pith. The transverse section through the internode shows two concentric series of five bundles each.

P. brachyphylla has decussating whorls of two leaves each. Each leaf contains three bundles, one median and two lateral. 'The median bundles run in the peripheral circle through two internodes, then turn inwards, and, after a further course in the pith through one internode, insert themselves with their tapering ends on a medullary bundle. All lateral bundles of the trace run through one internode in the peripheral circle, then curving in the next lower internode into the pith, they run further in the pith through one internode, and insert themselves, also with tapering ends, on the medullary bundles of the third internode.' In each node accordingly six bundles pass inwards; in the pith of the internode however there are only four: certain bundles must therefore unite on entering the pith. Weiss found the course similar, but more complicated and less regular, in P. rubella, and in P. variegata and incana, which have alternating leaves: of these the former has a leaf-trace of twelve bundles, the latter of seven.

Weiss, in common with Karsten, found in the woody Piperaceæ (Piper, Artanthe, species of Chavica) that the bundles of the many-bundled leaf-trace, which embraces the stem, descend, where there are *one* or two medullary circles, through at least one internode in the peripheral circle, then curving into the pith, they traverse a second internode in the medullary circle, and finally insert themselves on medullary bundles of a lower internode. On passing from the outer to the inner circle two or three bundles may unite, and the number of the medullary bundles may thus vary with little regularity in the successive internodes. Where there are more than two circles (Artanthe cordifolia) the medullary bundles traverse at least two internodes.

It is instructive that the course of the vascular bundles in the Piperaceæ closely resembles that of the Commelineæ (§ 69).

2. *All bundles belong to the leaf-trace. After entering the stem they pass over into a network of bundles, which branches irregularly on all sides.* To this series belong the Nymphæaceæ, Gunneraceæ, Primula Auricula, and its nearest allies, perhaps also many Balanophoreæ. In the first three groups a definite number of bundles are seen to enter the stem from each leaf, and immediately after entering they pass over into a network of bundles, which are irregularly connected both in the direction of the surface of the stem, and also in radial planes by oblique and

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Sanio, Botan. Zeitg. 1864, p. 193.—F. Schmitz, das Fibrovasalsystem d. Piperaceen, Diss. Essen, 1871.—J. Weiss, Wachsthumsverh., &c. d. Piperaceen, Flora, 1876.

transverse anastomoses, the network being still further complicated by the insertion of the bundles of roots and buds. Transverse and longitudinal sections through the stem show 'irregularly scattered' bundles, cut through in different directions; the former thus remind one superficially of transverse sections of stems of Monocotyledons, of which however only those of the Aroideæ with irregular reticulate connection of bundles can be more closely compared with them.

The structure of species of *Gunnera* has been more exactly investigated by Reinke[1]. In G. Chilensis Lam. (G. scabra R. B.) one bundle of the trace enters the short hypocotyledonary stem from each cotyledon: the two unite, after a perpendicular course, to form the axile root-bundle. The cotyledons are immediately followed by a pair of almost opposite primordial leaves, which decussate with them: then come the further leaves in spiral arrangement, all of them being separated from one another by extremely short internodes. From each of the primordial leaves three bundles, which unite in the cotyledonary node, enter the hypocotyledonary stem: here the two united traces alternate with those of the cotyledons, and unite with them lower down to form the axile bundle. Exactly at their point of entry into the centre of the stem they are mutually united by a horizontal bundle, parallel to the surface of the stem, and by one or a few, which traverse the middle of the stem obliquely. Branches from the latter pass to the cotyledonary bundles. From each of the leaves, which next follow the two primordial leaves, three bundles enter the stem, and from the successively higher ones a larger number (not exactly stated). Each successive leaf-trace resembles the first, inasmuch as immediately on entering the stem it is connected with the network of bundles by connecting bundles in all directions: only the number of bundles of every sort and direction increases in proportion as the axis of the seedling 2 mm. thick increases to the swollen stem of 50 mm. thickness. The appearance of the bundles of all categories takes place almost simultaneously.

In conformation and structure the following species coincide with G. Chilensis: viz. G. petaloidea, bracheata, insignis, commutata, peltata, manicata. G. perpensa L., to which is allied G. macrophylla, has in its stem of 1^{cm} in thickness, and with rather longer internodes, for the most part bundles with a longitudinal course: most of these are united into a hollow cylindrical net, within the parenchymatous cortex, and have transverse and oblique connecting bundles, which traverse the pith.

In the short internodes of the leafy stem of G. magellanica, which is 2–3 mm. thick, 3–4 vascular bundles run longitudinally: these are connected, directly with one another, by convergence, to form pointed elongated meshes, and also at the nodes they are united by transverse anastomoses, at the points of entry of the three-bundled leaf-trace. The elongated internodes of the stolons of this plant have usually only one concave band-shaped axile bundle: sometimes this splits for a short distance into two. Finally the thin stems of G. monoica and prorepens show in their internodes usually two bundles, which are here and there united to a single one, into which the (one-bundled?) leaf-traces run. In the elongated internodes of the stolons they have one axile bundle.

In *Primula Auricula*[2] the one-bundled leaf-traces of the cotyledons and of the first leaves unite, running almost horizontally into the middle of the stem, to form one axile bundle which traverses it. The bundles which enter from the subsequent leaves run for a distance—not defined by any constant number of internodes—side by side, and then unite with one another, or with the axile bundle. As the plant grows stronger the number of bundles entering one leaf increases to twenty, these pass obliquely down the stem, and are here united by irregular and oblique branches and anastomoses, which run

[1] Morphologische Abhandlungen, Leipzig, 1873, p. 47, Taf. 4–7.

[2] Vaupell, Ueber d. peripherische Wachsthum d. dicotyled. Rhizome, Leipzig, 1855.—Von Kamienski, Zur Vergl. Anatomie d. Primeln, Diss. Strassburg, 1875.

radially and tangentially. In transverse section there appears a ring of 15–20, widely separated, stronger bundles, which correspond to the central bundles of the base of the leaf: surrounding the ring numerous smaller bundles are irregularly scattered; these are derived from the lateral ones of the base of the leaf: in the space within the ring are seen the transverse sections of the connecting branches, which here also run in all directions. Pr. Palinuri, calycina, and marginata resemble Pr. Auricula. Other species of Primula, as Pr. sinensis, spectabilis, and elatior, have a typical Dicotyledonous ring of bundles, which are very soon united laterally by intermediate bundles. On their special course, and the peculiarities of many species, especially Pr. farinosa, compare Kamienski's work.

In the *Nymphæaceæ* the system of vascular bundles of the stem (Rhizome) is usually a network of anastomosing bundles difficult to disentangle, from which those for the leaves, roots, and peduncles branch off at certain places, and which in stronger stems, e. g. of Nuphar luteum, traverse the whole internal part of the stem, which lies within a sharply limited cortex, even to its very centre. It may be seen from Unger's figure[1] how chaotic this structure is. Nägeli (*l. c.* 121) tried to explain the matter by the investigation of weaker rhizomes of Nymphæa alba. I reproduce his description as follows. Internodes shortened. Leaves arranged spirally. The transverse section shows between pith and cortex a circle of separate bundles, which is divided usually into three, rarely into four groups, which can be recognised with the naked eye. The three groups are of unequal width: they vary continually throughout the length of the stem, and are related to the arrangement of the leaves. The bundles of the circle are often connected with one another, so that, when seen in surface view, they appear as a network. The middle of the pith is traversed by a central bundle, which throws off now and then a branch to the net-work.

From the base of the leaf five bundles enter the stem: three of these lie rather higher and form the true leaf-trace. Their lateral bundles separate widely from one another, and weave themselves in with the net-like circle at two almost diametrically opposite points, so that the trace is about 180° wide. The median bundle also loses itself usually at once in the net. But sometimes it passes inwards through the pith, after forming some anastomoses with other bundles, and unites with the central bundle. In one stem it was the 8th and 13th, in another the 1st, 6th, 11th, 18th, and 32nd leaves, the median bundles of which passed to the centre, while those of all the other leaves remained in the outer network. In the first example the 8th and 13th, in the second the 1st, 6th, 11th, and 32nd leaves were on the upper side of the procumbent stem, the 18th on its lower side.

An independent growth of the central bundle at its apex was not observed: Nägeli therefore considers it as a sympodium of median bundles.

I found in weak rhizomes of Nuphar pumilum that the transverse section resembled that described in the case of Nymphæa: an irregular ring of 8–12 bundles, and a central, often very eccentric, and frequently branched bundle being seen: the latter is in rare cases entirely absent from the section. The bundles of the ring form a net with elongated meshes, the main meshes being limited by the bundles of the leaf-trace, between which smaller bundles, usually pushed back rather further into the pith, form an irregular network. The leaf-trace consists of three bundles, and is about 120° wide, the median bundle forks in the node into two shanks diverging at an obtuse angle: each of these in its descending course is united with the lateral bundle of its own side. I never saw the median bundle curve to the middle line of the stem, but rather I here saw only a bundle, which ran irregularly from side to side, and here and there gave off a lateral branch and anastomosed with the peripheral net. An independent ending of this bundle beneath the growing-point was not to be found. Besides this I have examined but few preparations, and wished in the above remarks only to point to N. pumilum as an object well suited for the elucidation of the structure of the stem in the Nymphæaceæ.

[1] Anatomie und Physiologie, p. 235.

3. *Bundles of the trace and cauline bundles are both present. The bundles of the trace are arranged in a ring, the cauline bundles are in the pith.* To this series belong species of Begonia, Orobancheæ, species of Mamillaria, Melastomaceæ, some Umbelliferæ, and Araliaceæ: further in the main also Nelumbium.

In the *Begonias* medullary bundles are common. Hildebrand[1] found them in 28 species out of 128: for instance in B. Evansiana, laciniata, Rex, xanthina, etc. According to Hildebrand's description of stems in the mature state (following the course from below upwards) these seem to be for the most part caulíne. In the first internodes of the seedling they are wanting, they branch from those of the ring in higher internodes. They run parallel and perpendicular in the internode, in the nodes they anastomose with one another and with those of the ring: as a rule none pass through the node without connection with others. In B. Hügelii, Muricata, and luxurians Hildebrand saw 1–3 medullary bundles enter, without previous anastomosis with others, directly into the middle of the petiole, a phenomenon which occurs less frequently in others: e.g. B. laciniata. From the plexus in the node medullary bundles pass on into the next higher internode, and other bundles branch off to pass into the ring. In some stems single bundles in successive nodes pass successively into the pith, and again into the ring, and finally into a leaf, 'but this whole course is rendered very indistinct by anastomoses.'

The many points, which still remain doubtful, arise partly from the difficulty of following the course of the bundles in the Begonias with accuracy. It is made the more probable that the medullary bundles are for the most part cauline by the fact that, according to Sanio's investigation of B. Evansiana (*l. c.* 224), they appear later than those of the ring[2].

Aralia racemosa[3] and *A.* japonica have within the typical Dicotyledonous ring a second, consisting of small, widely separated bundles. In other species, e.g. A. papyrifera, the second ring is absent. Besides this ring there are, according to Sanio in A. racemosa, other single bundles scattered in the pith. All these bundles, which run perpendicularly in the internode, anastomose in the nodes without passing out to the leaves: their development proceeds much later than that of the ring. As regards the distribution of vessels and sieve-tubes the outer medullary bundles have a position the reverse of that of the bundles of the ring, the inner ones are irregularly arranged. Comp. § 101.

In the stem of some few *Umbelliferæ*[4], Silaus pratensis Bess., Peucedanum Oreoselinum Mch., Opoponax Chironium K., Ferula communis, and an undetermined form of Taurus, medullary bundles have been observed within the ring: as many as 13 in Silaus, 20 in Opoponax, 82 in the plant of Taurus (Reichardt), at least 100 in the flowering stems of Ferula communis. They are distributed in the transverse section over the whole pith: their number varies in successive internodes, e.g. in Silaus, Ex. I. 13, 11, 10, 9, 7, 3; Ex. II. 10, 8, 7, 7, 6, 1; Ex. III. 9, 8, 5, 3, 1: Peucedanum Oreoselinum, Ex. I. 22, 20, 18, 17, 14, 7; Ex. II. 20, 18, 17, 17, 12, 6; Ex. III. 15, 13, 10, 7, 3.

According to the consistent accounts of Jochmann and Reichardt the medullary bundles do not pass out into the petiole; they are cauline. They take a parallel and perpendicular course through the internode, dividing here and there, and united for short distances: at the node they anastomose by means of connecting bundles with one another, and with those of the ring: from the anastomosing bundles in the node those medullary bundles start which traverse the next internode. Those of the lowest internode above the root affix themselves on those of the ring of the same internode, or

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[1] Anatomische Untersuchungen über die Stämme d. Begoniaceen, Berlin, 1859.

[2] [Cf. Westermaier, Ueber das markständige Bündelsystem der Begoniaceen. Regensburg, 1879.]

[3] Sanio, *l. c.* p. 226.

[4] De Candolle, Organographie, I. p. 184, Taf. III.—Jochmann, de Umbelliferarum structura, 1854.—H. W. Reichardt, Ueber das centrale Gefässbündelsystem einiger Umbelliferen, Wiener Acad. Sitzungsbr. Bd. XXI (1856), s. 133.

rather spring from them: the same is the case with those of the lowest internode of a branch, so that the latter are not in direct continuity with those of the stem (Reichardt).

The occurrence of medullary bundles is a purely specific property. Of eight investigated species of Peucedanum they appear only in P. Oreoselinum: they are absent in Silaus tenuifolius. They are not present in the one-year-old seedling of S. pratensis.

Some *Mamillarias*[1] have, within the typical ring of bundles of the leaf-trace, a second in the peripheral parts of the pith, this being composed of numerous small cauline bundles. In M. angularis, and an undetermined similar species, there are about thirty of these. They ascend the stem parallel to those of the leaf-trace, are strongly undulated in a radial, and especially in a tangential direction, and anastomose at acute angles. They are absent in young seedlings and in young shoots, and appear later at some height above the base of the shoot, springing from the inner side of the bundles of the trace. I was unable to find anastomoses with the leaf-trace, or the ring of secondary wood, excepting at their point of origin. In other Mamillarias, as M. pusilla, glochidiata, &c., I looked in vain for the medullary bundles, even in the mature shoot. Of other Cactaceæ, forms of Echinocactus and thick ones of Cereus (e. g. C. candicans?) have a medullary system of bundles, which on account of its peculiar relation to the lateral shoots will be described in Sect. 94.

The small *Orobanchæ* have in their stems only the typical Dicotyledonous ring of vascular bundles. Strong stems of the more robust forms, as O. elatior Sutt., rubens Wallr., caryophyllacea Sm., Rapum Thuill., and Cistanche lutea[2], have, inside the ring, and scattered in the pith, small bundles, the number of which is variable, and is large in strong specimens. They are cauline, and in young specimens take an undulating longitudinal course through the stem, anastomosing here and there, and ending blind beneath the apex of the stem. Comp. Fig. 111. In fully developed flowering stems they gradually cease below the inflorescence, curving outwards, and uniting with the bundles of the ring. It is only in Cistanche lutea, where they occur in considerable quantity, that they run freely in large numbers to the extreme apex of the inflorescence. In *Epiphegus* americanus and *Conopholis*[3] there are found in the base of the main stem three concentric rings of bundles: in the latter genus the bundles composing them are contiguous with one another in radial series. It is uncertain whether these belong to this category, or to that of radially diverging bundles of the trace, or are products of a secondary cambium.

FIG. 111.—Orobanche Rapum (natural size). Bud of a flowering shoot, median longitudinal section. *b—b* ring of bundles, consisting of leaf-traces; within this are the cauline bundles. At the base, where it has been cut off, is a network of the latter, which anastomose one with another, and with the bundles of the leaf-trace.

In the flowering stems of species of *Balanophora*, according to Göppert's[4] description, the same or a closely similar arrangement occurs to that in O. Rapum: numerous branched bundles are scattered within a ring composed of bundles of the leaf-traces.

In the Helosideæ the ring of bundles is alone present in the elongated rhizomes, in the tubers and Inflorescences there are branched, scattered bundles[5].

Two cataphyllary leaves and one foliage leaf succeed one another regularly on the

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[1] Von Mohl, Verm. Schriften, p. 115.

[2] Graf zu Solms-Laubach, de Lathrææ generis positione systematica, Diss. Berlin, 1865, pp. 8, 14, and Pringsheim's Jahrb. VI. p. 522.

[3] Chatin, Anat. Comp. Taf. XVIII.

[4] Ueber den Bau der Balanophoren, N. Act. Carol. Leop. vol. XVIII. Suppl. 1.—Compare also Hooker, Balanophoreæ, Trans. Linn. Soc. London, XXII; Graf zu Solms, in Pringsheim's Jahrb. *l. c.* p. 529.

[5] Compare Eichler, in Flora Brasiliensis, Fasc. XLVII.

rhizome of *Nelumbium* speciosum[1]. The internode between the latter and the next following scale leaf is elongated (as much as 4 feet), the others are short. The elongated internode (Fig. 112) has six blunt angles, so that when horizontally placed one surface is turned upwards (*o*), another downwards (*u*), and one edge to each side right and left. It is traversed by 6 large air-canals (*l*), corresponding to the angles, one small axile one, and two small ones, corresponding to the upper surface, and in regular cases (slight deviations occur) by about 252 vascular bundles with a perpendicular course, the arrangement of which in the transverse section is according to Wigand as follows. Firstly, an *inner* system of twelve bundles, disposed in two concentric alternating circles (1 and 2) of six each, at equal distances from one another in each circle, in the inmost circle (1) one bundle is opposite the upper, and one opposite the lower surface; secondly, a *middle* system, extending to the outer limit of the air-canals: it consists of four concentric rings (circles 3–6); in each of the circles 4, 5, 6, one bundle alternates with two air-canals: in circle 3, in addition to the otherwise similar arrangement, there are on each side between each two

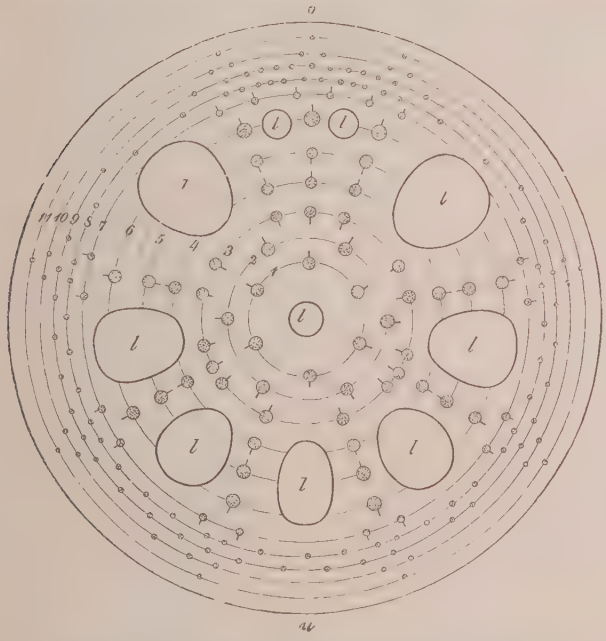

FIG. 112.—Scheme of the transverse section through the internode of a rhizome of Nelumbium speciosum, after Wigand. *o* upper, *u* lower side; *l* air canals. The figures 1—11 indicate the successive circles in which the bundles are arranged. The bundles of the circles 3 and 5 have an orientation the reverse of that of the others, which is indicated by direction of the dashes affixed to the round spots.

lateral lower air-passages three bundles, and on each side between the two lateral upper ones two bundles, that is six more bundles are present than in the other circles: the bundles of four circles, with exception of the last-named six, form regular radial rows. Thirdly, the peripheral system, between the outer side of the air-canals and the surface of the stem, consists of 4–5 concentric circles of bundles (7–11), the inmost (7) having 18 bundles in pairs alternating with the radial rows of the middle series and with the air-passages; the next (8) consisting of 45 bundles, of which two are between the two of one pair, and

[1] According to Wigand, Nelumbium speciosum, Botan. Zeitg. 1871, p. 816, &c. See also Trécul, Ann. Sci. Nat. 5 sér. I. p. 162, &c.

three between each two pairs of the above; the bundles of the next (9) alternate with those of (8), those of (10) and (11) alternating irregularly with those next within them.

Of these bundles all those of the peripheral series are, according to Wigand, 'true leaf-bundles, since they traverse only one internode and then run into the leaf-organs.' The course of the rest is difficult to describe with certainty, because of the complicated branchings of lateral shoots and roots in the node, and it requires further investigation. The bundles of the inmost circle of the middle series (3) seem to be cauline, since 'it has not hitherto been possible to prove that they contribute to the lateral organs,' and they 'apparently always traverse one internode only, and lose themselves in the node, their place being taken by fresh ones in the following internode.' The same holds perhaps for the other members of the middle series, which are radially arranged. Of the inmost series the four lateral bundles of the inner side (1) give off branches to the roots, the upper and under ones of the same circle give off branches 'directly or indirectly' to the leaves. All six bundles of this circle 'are however distinguished by the fact that they alone of all the bundles of the stem traverse all internodes and nodes up to the growing point,' while on the contrary the six bundles of the same series, which alternate with them (2), 'each belong to one elongated internode only, and to the roots (which arise at each node), and then end in the node, just above the root-region.'

The medullary bundles of the *Melastomaceæ* will be described below, p. 259, in connection with the rest of the bundle system of these plants.

b. *Cortical bundles.*

Sect. 63. A relatively small number of Dicotyledons is characterised by having a bundle system in the internodes arranged typically in a ring, and outside this other bundles, which traverse the cortex. These cortical bundles are sometimes bundles of the leaf-trace, which run for a certain distance outside the ring, and later curve into it: as in the cases of Lathyrus Aphaca, and Pseudaphaca above described, the Casuarinas, and many Begonias: also the cortical bundles of the Cycadeæ, to be described in detail in Chap. XVI, belong to this category, perhaps also Nepenthes. Sometimes they are certain bundles, belonging to many-bundled leaf-traces, which never enter the ring, but form with the similar ones belonging successively to upper and lower leaves an independent cortical bundle-system only connected with the ring by anastomoses at the nodes: this is the case in the Calycantheæ, many Melastomaceæ, also in Arceuthobium Oxycedri. In many succulent plants with reduced leaves, as Salicornia, Cacteæ, they are branches of the bundles of the leaf-trace, which are branched and distributed like the bundle-expansions of the leaf lamina, and will therefore be treated of where these expansions are described. Finally, in the winged Rhipsalidaceæ, according to Vöchting, the peculiar case occurs that the bundles of the leaf-trace are mainly cortical, while a ring of bundles, surrounding a pith, and quite similar to the typical Dicotyledonous ring of bundles of the leaf-trace, consists at least for the most part of cauline bundles.

The young foliage shoots of the **Casuarinas**[1] (Fig. 113) are covered with whorls of small leaves, united into a long sheath: the average number of leaves of one whorl varies according to the species (4–20). The leaves of successive whorls, and the ridges, which run down the backs of the leaves, alternate in successive internodes. One vascular bundle enters each leaf. From the point of insertion of the sheath it passes

[1] Compare Löw, De Casuarinearum caulis foliique evolutione et structura, Berlin, 1865.

into the periphery of the stem, and there runs, parallel to it, in the cortex as far as the next node: it then curves inwards, and ranging itself with those of the same whorl of leaves around a narrow cylinder of pith, it descends perpendicularly through a second internode. At the lower limit of this, i. e. at the 2nd node from the point of exit into the leaf, it is inserted (according to Löw with a short fork) on the bundles which here pass out into the cortex. The transverse section of each internode thus shows 2 concentric circles of an equal number of alternating bundles: the one peripheral, composed of the bundles of the trace of its own whorl of leaves, the other axile (forming the woody ring at a later period), consisting of the bundles of the trace of the next higher leaf.

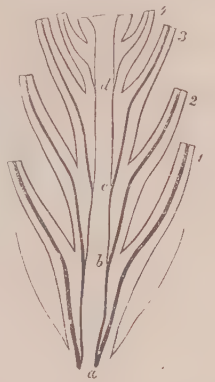

FIG. 113. — Casuarina muricata. Scheme of the course of the vascular bundles in the median longitudinal section of a young branch. 1—4 successive whorls of leaves; bundles of whorl, 2 ending in node *a*, 3 in *b*, 4 in *c*, &c.

In *Begonia* angularis Raddi, Hildebrand[1] found one bundle in the outer cortex of each of the six angles of the stem. All the six in one internode form together the trace of the next higher leaf, which includes $\frac{5}{6}$ of the circumference of the stem. They pass perpendicularly downwards in the angles to the next lower node, and here curve into the ring of bundles. Their further course in the latter has not been investigated. Many internodes have less than six angles, and correspondingly fewer cortical bundles: others may be entirely without either. The same is the case with Begonia tomentosa, with this difference, that the number of the cortical bundles is 'indefinite' and often very large, while some of them often run through two internodes in the cortex.

Arceuthobium Oxycedri[2] has decussating pairs of leaves, each leaf has three bundles of the trace, one median and two lateral. The latter converge, and enter the stem: here they unite and descend opposite those of the other leaf of the pair, and separated from them only by a narrow band of pith, to the next node, where they insert themselves upon the bundles which there pass out. The thin median bundle of each leaf pursues an individual course through the cortex, and is also inserted at the next lower node. The transverse section through an internode thus shows two decussating pairs of bundles, one stronger axile pair, and one weaker and peripheral.

In the *Calycanthaceæ*[3] three bundles pass out into each of the opposite and decussate leaves, one stronger median, and two weaker lateral ones. The median ones are arranged in a ring in the stem. Each runs down through two internodes, and then affixes itself at the node on the median bundles which there pass out. The lateral bundles (rather later developed) pass perpendicularly down the stem in the cortex outside the ring of bundles: at the next node they insert themselves on the cortical bundles which there pass out. Thus in each internode the transverse section shows the ring of bundles, and outside it four cortical bundles. In the node each cortical bundle is connected with the ring by a short radial transverse bundle, and by another with the median bundle which next passes out, and again, by a stronger horizontal girdle-like bundle, with the next cortical bundle belonging to the same side of the stem.

In the seedling two bundles enter each cotyledon: they descend with the median bundles of the first three leaves through the hypocotyledonary axis, the transverse section of which thus shows six bundles. The cortical bundles of the first two leaves only extend down to the cotyledonary node.

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[1] *l. c.*, compare p. 253.

[2] Graf zu Solms-Laubach, in Pringsheim's Jahrb. Bd. VI. p. 523.

[3] Mirbel, Ann. Sci. Nat. XIV (1828).—Gaudichaud, Archives de Botanique, II. p. 493 (1833). —Woronin, Botan. Zeitg. 1860, p. 177.

In the internode of *Nepenthes*[1] there is found an inner typical bundle-ring, surrounding the pith, which later undergoes secondary thickening, and externally other bundles are

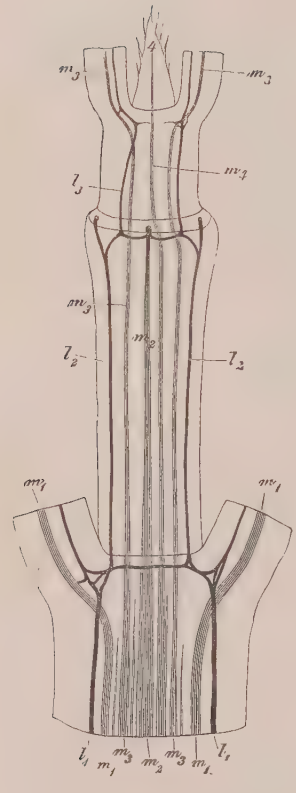

FIG. 114.—Centradenia rosea. End of a shoot, halved longitudinally; the three lower pairs of leaves and the epidermis removed, made transparent by potash, and seen from *without*. The pairs of leaves and the bundles belonging to them numbered in order; *m* the median ones, *l* the lateral bundles. One leaf of the fourth pair (4) covers the growing-point. In the node of pair 3 the transverse girdle is as yet imperfectly developed. Further description in the text. Magnified about 25.

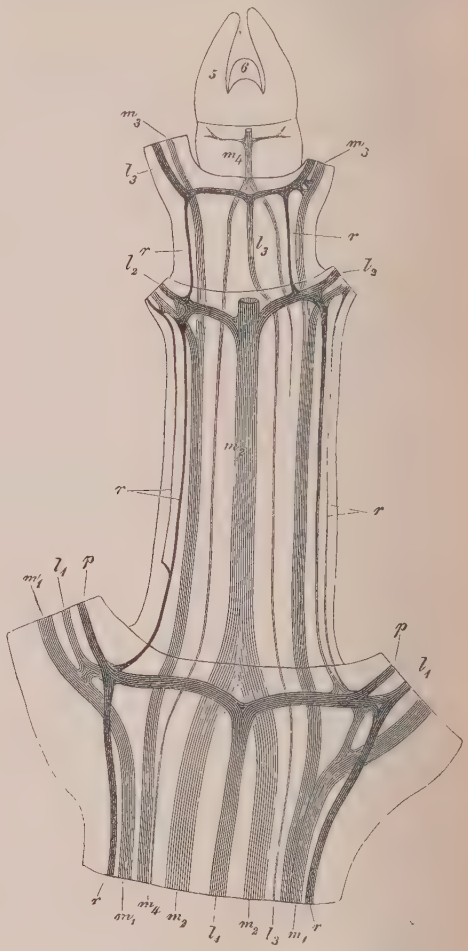

FIG. 115.—Osbeckia canescens (magnified about 25). Longitudinal half of the end of a shoot, prepared like Fig. 114, and seen from without. Six decussating pairs of leaves numbered in order; in 5 and 6 as yet no bundles, in 4 the median bundle is just visible. Further description in the text.

to be seen in the very broad outer cortex: these are partly bundles of the leaf-trace, which passing in a radially-oblique direction through the cortex, gradually enter the

[1] C. H. Schultz, Vaisseaux du Latex, *l. c.*, compare p. 249.—Korthals, Verhandelingen, *l. c.*, compare p. 226.

inner ring; partly small bundles, the origin of which remains to be decided; these pass close beneath the epidermis, and are connected with one another by oblique branches. A thorough investigation is in progress[1].

In the *Melastomaceæ* the course of the cortical bundles is partly the same as the above, and partly similar to that in Calycanthus. It may here be described in connection with the other peculiarities of arrangement of the bundles in this family (comp. p. 256)[2].

The stem has four angles, and bears decussate pairs of opposite leaves: those of one pair are either equal, or, as in many Centradenias, of unequal size. Each pair faces two opposed surfaces of the stem: these may be called the surfaces belonging to that pair, and the others the intervening surfaces. In the simplest case investigated the trace of the single leaf which enters the node consists of three bundles, one median and two lateral: in many species it consists of more than three, through multiplication of the lateral bundles on each side. The bundles which enter the stem pass, in many species, directly into the bundle-ring without forming cortical bundles: Sonerila margaritacea, Medinilla farinosa, Sieboldii, magnifica, Cyanophyllum magnificum, Clidemia parviflora, Miconia purpurascens, Lasiandra Hoibrenkii[3]. In the other investigated species the median bundle always enters the bundle-ring, usually without, rarely after previously giving off cortical bundles; the lateral ones either run, as in Calycanthus, down the angles of the stem as cortical bundles, or they enter the ring, after having given off cortical bundles as branches. The cortical bundles are always connected at the node both with one another and with those which pass to the ring, by a transverse girdle of horizontal branches: they run from this to the next lower transverse girdle, and insert themselves on the latter. In the ring the bundles of the trace always pass down through several internodes, they pectinate in various ways with those of lower pairs of leaves, remaining simple, or splitting into shanks. For numerous differences of arrangement according to the number of bundles and the species, compare Vöchting, *l. c.*

The cortical bundles are always derived, as above stated, from the bundles of the trace. In the simplest case (Centradenia rosea, Fig. 114) they are the lateral bundles of the three-bundled trace. From the base of the leaf one stronger median bundle ($m_1 - m_4$) and two weaker lateral ones enter the node. All the median bundles are arranged in the ring: they pursue an individual course, directly, or with slight curvature at the nodes, through three internodes (two according to Vöchting), and then unite laterally with such as come from lower nodes. The lateral bundles give off one branch on each side at the node, which runs transversely through the outer cortex, the one to the out-going median bundle of the same leaf, the other to a similar one, which comes from the nearest lateral bundle of the opposite leaf. These branches together form the transverse girdle of the node, which girdle is further connected with the out-going portions of the bundles by small branches. From the point of departure of the branches of the girdle each lateral bundle runs perpendicularly through the cortex of the corner of the stem, and inserts itself on the transverse girdle of the next lower node.

As an example of the other case, i. e. that cortical bundles and transverse girdles are branches of the bundles entering the ring, Osbeckia canescens (Figs. 115, 116) may be described. A strong median bundle $m_1 - m_1$ enters from each leaf, into the corresponding side of the internode, and here descends perpendicularly, in the bundle-ring: in the next lower node it splits into two shanks (m_2 and m_4), which enclose between them the united lateral bundle, which there enters the stem: these shanks may be further followed down three internodes. A strong lateral bundle passes from each leaf almost horizontally through the cortex into the middle of each of the intervening sides: it here unites with

[1] E. Zacharias, Ueber die Anatomie des Stammes der Gattung Nepenthes, Strassburg, 1877.

[2] Vöchting, Bau, &c. d. Melastomaceen, in Hanstein's Bot., Abhandl. III. Compare also Crüger, Botan. Zeitg. 1850, p. 178.—Sanio, Ibid. 1865, p. 179.—Hildebrand, Begoniaceenstämme, p. 1.

[3] The names quoted are partly derived from Vöchting's work, and partly garden names, for the correctness of which I will not answer.

a similar one from the opposite leaf, and the united bundle (l_1–l_3) then curves into the ring. Its course in the ring may be gathered from Fig. 115. The lower endings of the bundles in the ring were not investigated. Opposite its point of exit into the leaf the median bundle gives off a branch on either side, which takes a curved and almost horizontal course through the cortex to the nearest angle, and here unites with the out-going lateral bundle. The transverse girdle accordingly arises from the last-named branches of the median bundles, and the horizontal portions of the lateral ones. From the latter sections of the girdle there arise near each angle one or two cortical bundles (*r*), which run perpendicularly to the next lower node, and here insert themselves on the transverse girdle. If two cortical bundles are present, they stand radially before one another, and one often inserts itself on the other before reaching the lower girdle. To the above description it may be added that the two lateral bundles which have been mentioned in each leaf-trace are each formed by the coalescence of two lateral bundles (*l* and *p*, Fig. 115) of the base of the petiole.

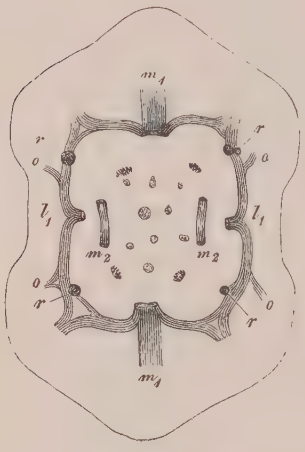

FIG. 116.—Osbeckia canescens. Thick transverse section through a node, which is rather further developed than 3 and less than 2 in Fig. 115; it is transparent, and seen from below. The transverse sections of the bundles of the leaf-trace which are nearest the beholder and in the surface of section are represented as *dark*. m_1 the median bundles of the trace passing out at the node; *l* the lateral bundles of the same; *r* the cortical bundles which pass down from the node; *o* those which pass upwards from it; m_2 the median bundles of the next higher node, which branched above the node; with them there alternate, opposite each corner, single bundles, with regard to which it is not quite certain whether they are the lateral ones of the next higher pair of leaves, or shanks of the median bundles of the second higher pair. The lighter spots in the pith indicate the transverse sections of the cauline bundles. In this node they were not yet plain, and have been drawn in the figure from another preparation (40).

For further peculiarities in other species reference may be made to Vöchting's work: it may be added that the examples here selected have been retained, since the corresponding woodcuts were finished two years before that work appeared. Species with wide wing-like projecting angles often have several cortical bundles placed radially one before another in each of these angles (e. g. Heterocentron subtriplinervium, Lasiandra macrantha 3–4, Centradenia grandifolia 5–7), these anastomose now and then with one another; they originate as branches either of median or lateral bundles of the first order, or from lateral bundles of a higher order, if such are present.

Besides the cortical bundles there are also cauline medullary bundles in most of the Melastomaceæ (compare Fig. 116). These are usually to be found also in those species in which the cortical bundles are absent. Only Sonerila margaritacea is without either: it alone of the species investigated has a quite typical Dicotyledonous bundle-system. In the simplest case a single bundle is found in the centre of the pith, e. g. Medinilla farinosa, Sieboldii, or this may even be sometimes present, sometimes absent, as in Eriocnema marmorata and Centradenia rosea. In the transverse section of the internode of other species there are several bundles which lie in the middle of the pith, e. g. Melastoma igneum, Lasiandra Maximiliani 1–3, Medinilla magnifica 2–4, Melastoma cymosum 8–10; finally, others have many of them scattered over the whole transverse section, e.g. Heterocentron subtriplinervium 18, Miconia chrysoneura and Cyanophyllum magnificum 30, 40, and more.

The medullary bundles run perpendicularly through the internodes. In the nodes they are connected by oblique or transverse branches of varying number one with another, and with the bundles of the ring. From the network or felt thus formed proceed those of the next higher internode. In the large majority of cases they arise much later than the bundles of the leaf-trace which are in the same transverse section, and they do not pass out to the leaves. The medullary bundles are usually relatively small, and characterised by peculiarities of structure to be described below (§ 105).

Some of the *Rhipsalideæ*[1] have round stems, others angular and winged; both forms have in transverse section a circular or elliptical ring of bundles, which, especially in the winged species, is surrounded by a very broad succulent cortex. In the round forms, such as R. Saglionis, salicornioides, the one-bundled leaf-traces pass slightly obliquely downwards through the cortex into the ring, which is originally formed from them alone, but later secondary intercalary bundles also appear (Chap. XIV). In the winged forms the leaves are seated only on the angles. The bundles of the trace enter these, and run, in the main tangentially-perpendicular and radially-oblique, down through the cortex; they enter the ring about the level of the next lower leaf, and then descend further in a perpendicular direction. They thus form the portions of the ring corresponding to the angles. But the portions of the ring between these, which correspond in the elliptical ring of two angled forms (e.g. Lepismium radicans, Rhipsalis carnosa), to the broad sides of the ellipse, as seen in transverse section, and which comprise the greater part of the ring, are here composed of cauline longitudinal bundles, connected here and there by oblique anastomoses: on these the common bundles insert themselves in the region indicated. These cauline bundles correspond to the secondary intercalary bundles, which complete the woody ring of typical Dicotyledons, and which will be described in Chapter XIV; but they are distinguished from these by their appearing on the first primary differentiation of tissues. Finally, in all Rhipsalideæ branches come off from the bundles of the trace during their course through the cortex: these with their further branches form a cortical network of bundles (which is further strengthened by the bundles which come from the axillary buds). The special form and development of this varies according to the species, in the winged species it is exclusively or chiefly expanded in the wings, in a radial direction. Compare Vöchting, *l.c.*

It is not known how far other Cactaceæ, which are winged and have a cortical network of bundles, correspond to the winged Rhipsalideæ in the course of the bundles of the leaf-trace and intercalary bundles.

III. The Type of the Palms.

Sect. 64. The stem of most Monocotyledons does not show the bundles in the transverse section of an internode arranged in a simple ring, but within a peripheral zone of *cortex*, which has no bundles, there is a circular surface, in which either several concentric irregular and interlocking series of bundles are arranged round a central portion without bundles (pith), as e.g. in many stems of Grasses, which later become hollow; or the bundles lie scattered over the whole surface. Thus instead of the ring of bundles of the Dicotyledons there is here a *cylinder*, which contains the bundles; the zone surrounding the cylinder, which was called the cortex, corresponds to the cortex of the Dicotyledons: the terms pith and medullary rays may be used in a comparative sense for the bands of other tissue (as a matter of fact parenchymatous) which lie between the bundles in the cylinder.

The arrangement of the bundles in transverse section in the Palm type depends upon the radially-oblique course of the leaf-traces. This must first be demonstrated for that form which may be called the simple Palm type: with this are further connected a number of more or less divergent phenomena.

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[1] Vöchting, Morpholog. und Anat. d. Rhipsalideen, Pringsheim's Jahrb. IX. p. 326.

a. *Simple type of the Palms.*

Since Mohl's Anatomy of Palms[1] the following chief characteristics have been known for this type.

All bundles of the cylinder (with doubtful, and extremely unimportant exceptions to be mentioned below) are bundles of the leaf-trace. The base of the leaf encloses the whole circumference of the stem, or at least the greater part of it. The leaf-trace always consists of a number of bundles, and usually of many, in strong shoots of two hundred bundles: its width is $\frac{1}{1}$ of the circumference of the stem, or more, or not much less. The bundles curve from the base of the leaf into the cylinder, and pass downwards in the latter; some at its surface, running almost radially perpendicular; others are radial and oblique, penetrating first in a curve convex upwards and inwards, towards the longitudinal axis of the cylinder, then turning outwards and gradually passing towards the surface of the cylinder; as they approach it, they assume an almost perpendicular position. All bundles descend through many internodes, and finally unite in the outer portions of the cylinder with such as emerge lower down, inserting themselves on these sometimes in a tangential, sometimes in a radial or oblique direction. Up to this point of insertion at their lower ends the bundles pursue an individual course. The coalescence of the lower ends of descending bundles with such as emerge lower down occurs with such frequency that the whole number of the bundles in equally strong successive internodes remains about the same. Where the successive internodes and leaves grow stronger the number of the bundles increases, and *vice versa*. The number of the internodes which a bundle traverses cannot be exactly defined.

Further, the bundles of a leaf-trace, which curve towards the middle of the cylinder, do not all penetrate to the same depth; on an average the median bundle of a series penetrates the deepest, the others less deeply the further they are from the median one, the marginal ones pass almost perpendicularly down the surface of the cylinder: where there are several series, those of the inmost penetrate as a rule deeper than those of the outer, which are equally distant from the median bundle.

The necessary consequences of the course described are, firstly, that the bundles in the transverse section of an internode are more crowded the nearer they are to the surface of the cylinder, a phenomenon which is especially striking where the bundles are distributed over the whole surface of section of the cylinder. Secondly, that the successive traces pectinate, and cross one another with their curved bundles. Mohl's celebrated scheme, which is here reproduced in Fig. 117, shows this condition in radial longitudinal section, but starting from the incorrect assumption that all bundles of one trace are almost equally curved and are tangential and perpendicular, that is that they lie at the surface of a cone which has a funnel-shaped opening at the top. If it is assumed that the leaves alternate with a divergence of $\frac{1}{2}$ and embrace the stem, and that the bundles are tangentially perpendicular, their course in the stem would be represented with greater exactitude by the scheme of a radial

[1] De Palmarum Structura; Monachii, 1831; Verm. Schr. p. 129; translated in the Ray Society's Reports and Papers on Botany, 1849.—Nägeli, Beitr. I. *l. c.*

section through the median planes of the leaves, Fig. 118. But the assumption of a tangentially-perpendicular course only holds good for bundles which are also radially perpendicular. As Meneghini[1] first asserted, and Mohl also conceded (Verm. Schriften, p. 160), and as Naegeli proved more accurately, each radially curved bundle runs also tangentially oblique, with a spiral curvature, which is stronger the stronger the radial curvature. Nägeli found e.g. that the median bundle of a leaf of Chamædorea elatior Mart. made $1\frac{1}{8}$ revolutions in passing through six internodes: in the sixth it had not quite accomplished half the distance from the centre of the stem to the inner surface of the cortex, on its way outwards. In stems with very short internodes and closely packed bundles the spiral curvature is at once visible in the transverse section, and very plainly in the bundles of the stem of Xanthorrhœa,

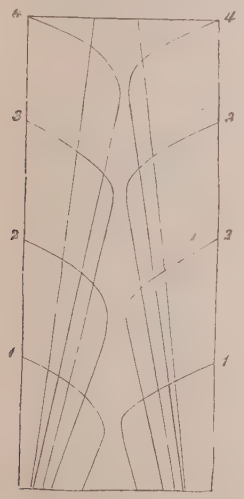

FIG. 117.—Mohl's scheme of the vascular system of Monocotyledons. Successive leaves, or rather successive nodes, are numbered in order.

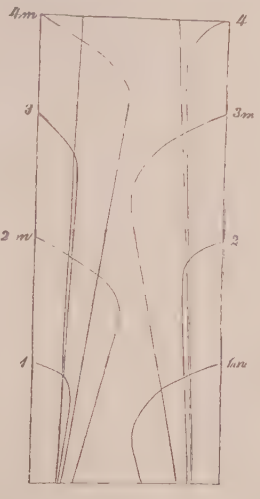

FIG. 118.—Scheme of the vascular system in the Palm-type, assuming that the leaves alternate in two rows, and embrace the stem. Successive leaves numbered in order. *m* median bundle.

which pass almost horizontally to the middle of the stem: the peculiar appearance so often noted[2] in transverse sections of this plant depends upon the above peculiarities.

Finally, many variations of direction from that hitherto described as uniform may occur in the course of a bundle, such as curvatures outwards and inwards, &c., which never appear to be constant.

The above description holds both for the preponderating number of cases, in which those bundles which penetrate deepest reach the middle of the stem, and also for those where, as in the stems of grasses which become hollow, a broad central part (pith) remains free from bundles. Where the internodes are short, as e.g. in the well-known preparations by maceration of the stems of Dracæna Draco, the course can easily be recognised in the main features. Where the internodes are

[1] Ricerche sulla struttura del caule nelle piante monocotiledoni, Padova, 1836.

[2] De Candolle, Organographie, I. Tab. VII. VIII.—Schleiden, Grundzüge, 3. Aufl. II. p. 160.

very long and thin, as e.g. in the Grasses, or egg- or spindle-shaped, as in the so-called pseudo-bulbs of epiphytic Orchids, it appears otherwise at first sight. The internode appears to be traversed by bundles, which are parallel, or convergent towards both ends: of these some may be seen to enter the leaf at the node, while many run into the next internode. One may however be easily convinced that here also their course is such as that above described. In young stems, which are still short, no variation from it is to be traced. In the subsequent elongation of the internodes of the stem of Grasses to 20–50 times their original height or even more, that portion of all the bundles which turns outwards while descending is so elongated, that at first sight it does not appear to deviate from the perpendicular in any one of the six or more internodes which it traverses: the general view of its course is rendered especially difficult by a complex felt of transverse bundles in each node[1] (comp. Sect. 95). In the pseudo-bulbs besides this elongation there is also a transverse swelling of the internode in the middle, and a consequent curvature of the bundles.

According to the statements of Unger[2] and Millardet[3] there is found in plants of this category, Grasses, Palms, Dracæna, Yucca, Narcissus, Galanthus, Leucojum, Pandanus, in addition to the bundles of the leaf-trace a further system of cauline bundles, which run upwards outside the cylinder, converging towards the growing-point; according to the rule which holds for cauline bundles in the Phanerogams, these are formed later than the bundles of the leaf-trace. Leaving out of account the Commelinaceæ, which will be described below, and the secondary formation of wood in Dracæna, Yucca, and their allies, I could not convince myself of the presence of such cauline bundles, which might it is true be easily mistaken for perpendicular bundles of the trace.

As has been repeatedly stated, the cylinder traversed by the bundles is in most of these cases sharply marked off from the inner surface of the cortex. The cortex itself is of variable thickness, in Rhizomes it is usually of great thickness, in aerial stems it is often relatively very thin.

b. *Modifications of the type of the Palms.*

Sect. 65. According to the scheme laid down in the previous paragraphs all the bundles pursue an individual course up to their point of final insertion at the periphery of the cylinder, this being sharply limited from the cortex, which in the internodes is without any bundles.

In many cases this scheme is subject to the following modifications: (1) the bundles receive oblique or transverse connecting branches, or anastomoses, during their course: (2) before they reach the periphery of the cylinder in their curved course they unite with others belonging to lower leaves (Sect. 66): and (3) cortical bundles appear outside the cylinder (Sect. 67). Each of these phenomena may occur separately or combined with the others.

Anastomoses of the bundles of the leaf-trace one with another—besides those

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[1] Von Mohl, Palmarum Structura, Tab Q.—Schleiden, Grundzüge, 3. Aufl. II. p. 158.

[2] *l.c.* p. 54.

[3] Mém. de la Soc. des Sciences Nat. de Cherbourg, tom. XI. p. 4.

which arise through the insertion of bundles which go to the branches and roots—occur in the greatest abundance, so as completely to mask the typical course of the bundles, in the tuberous stems of certain Aroideæ to be described below. In other stems with short or slightly elongated internodes they appear as an unimportant phenomenon which occurs occasionally. They are however numerous and characteristic in the greatly elongated internodes of the flower-stems and foliage shoots of many Cyperaceæ, Scirpus palustris, lacustris, and their allies, of Papyrus, species of Cyperus, and of Pontederia cordata[1]. These 'halms' have this peculiarity, that their longitudinal bundles are connected in a reticulate manner one with another by small horizontal or oblique branches, like those of the foliage-leaves of Monocotyledons (Sect. 91). The transverse branches run in the diaphragms (but not by any means in all), which separate the air-cavities one from another. According as the longitudinal bundles are scattered over the whole transverse section of the halm, or (as in Sc. palustris and its nearest allies) only form a ring inside the chlorophyll-parenchyma of the cortex, there are found also transverse branches throughout the whole thickness of the halm, and in the most various directions, or only in the zone occupied by the ring.

Sect. 66. The phenomenon of insertion of bundles of the leaf-trace during their curved course through the middle of the cylinder, and before they reach its periphery, on others which emerge lower down, and of their further descent in union with the latter, is also of frequent occurrence in the Aroideæ to be described below. Further it occurs in Pandaneæ[2], Bromeliaceæ (Ananassa, Tillandsia acaulis, Hort.), and apparently also, according to Karsten[3], in many Palms, especially Martineza aculeata. Whether this union of their course follows definite rules for certain bundles of a leaf-trace remains for more exact investigation to decide.

Sect. 67. The cortex is free from vascular bundles in many of the Monocotyledons of this category, if those bundles be disregarded which pass to the leaves at the nodes, and those which enter branches and roots: such bundles must appear in all or almost all transverse sections where the internodes are very short. On the other hand a special cortical system of bundles may be distinguished from the cylinder in certain cases. This consists in the simplest case of bundles of the leaf-trace, which after their entry into the stem descend first in the cortex through one or several internodes, and then enter into the cylinder. This is the case in stems of certain Aroideæ, in many Rhizomes, as Carex hirta (but not in C. disticha), where all bundles run through one internode in the cortex: Scirpus lacustris, Typha, Sparganium, &c. In other cases however it consists of bundles, which do not take part, or at least not directly, in the construction of the cylinder: Palms, Scitamineæ, and many Bromeliaceæ.

In the cortex of those Palms which have been investigated, small bundles, which are arranged in irregular concentric rings, are found in the cortex, outside the dense periphery of the cylinder. P. Moldenhawer has compared the region in which they lie with the bast of Dicotyledonous trees (Chap. XIV), Mohl has named it the

[1] Duval-Jouve, Diaphragmes vasculifères, *l.c.*; compare p. 216.
[2] Van Tieghem, Ann. Sci. Nat. 5 sér. tom. VI. p. 195.
[3] Karsten, Veget. Org. d. Palmen, p. 98.

fibrous layer. It is weakly developed in tubular stems like Calamus (Geonoma, Bactris, Hyospathe, Desmoncus, Calamus), and in the cylindrical stems of Mohl (Mauritia, Oenocarpus, Kunthia, Astrocaryon sp., &c.): more strongly in Rhapis flabelliformis, Phœnix, Jubæa spectabilis [1]): and most fully developed in Mohl's Cocos-like stems: Cocos, Leopoldinia, Syagrus, Elais, Corypha sp. Mohl regards the bundles of the fibrous layer as being, at least in part, bundles of the leaf-trace, the lower ends of which pass out from the cylinder into the cortex, and pass down to the base of the stem as fine threads, either undivided, or split up into many thin branches (Cocos).

More recent investigations [2] have shown that the bundles of the fibrous layer are not the ends of bundles which pass through the cylinder and emerge from it lower down, but that, as Mohl [3] also allowed to be the case with some of them, they pass from the base of the leaf directly into the fibrous layer. Here they run almost perpendicularly, and frequently show splittings and branchings, or fusions; the latter especially in a tangential direction, both in the internodes, and also in the insertions of the leaves, so that those bundles which enter from a leaf are in direct continuity with those which descend from higher leaves. Most of the bundles in question in the fibrous layer consist of a number of sclerenchymatous fibres: in a strict sense therefore they do not belong to this category. But in others according to Mohl's figures, and according to investigations on species of Chamædorea and Rhapis, there are solitary small sieve-tubes, and in single cases also one or a few small tracheæ. And while some continue as purely sclerenchymatous bundles into the petiole, others, after their entry into the petiole, assume the structure of fully organised vascular bundles [4]. Further, according to a note by Schacht, there is a connection with or transition to the vascular bundles of lateral roots, though the fibrous bundles do not arise 'as branches' of these.

The cortical system of bundles of the Palms is accordingly a direct continuation both of the system of vascular bundles, and of the system of purely sclerenchymatous bundles in the leaves, and connects them one with another.

Another cortical bundle-system occurs in the stem of *Ananassa* and *Tillandsia* acaulis Hort. The parenchyma of the thick cortex is here traversed by numerous bundles of the trace, which pass obliquely downwards from the leaves into the sharply limited cylinder. Other thin but also complete vascular bundles pass from the base of the leaf into the cortex: here they pass down, sometimes close beneath the surface, sometimes deeper, but always far removed from the cylinder, through several internodes, and then insert themselves on one of the main bundles, and with it enter the cylinder. The general direction of their course is approximately perpendicular, or arched according to the dome-like shape of the end of the stem: they are besides curved in a sinuous manner to a very variable extent. It is doubtful whether the anastomoses of the bundles of Ananassa, described by Unger [5], are these cortical

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[1] Wossidlo, Quædam additamenta ad Palmarum anatomiam, Diss. Vratisl. 1860, and Nova Acta Leop. Carol. vol. XXVIII.

[2] Schacht, Lehrbuch, I. p. 327.—Nägeli, *l. c.* p. 132.—Wossidlo, *l. c.*

[3] Palmarum Structura, p. xviii; Verm. Schriften, pp. 155, 184.

[4] Mohl, Wossidlo, *l. c.*

[5] Dicotyledonenstamm, p. 50, figs. 23, 24.—Anatomie und Physiologie, p. 232.

bundles, or the above-mentioned isolated communications which occur within the cylinder.

In most Scitamineæ (Musaceæ, Zingiberaceæ, Cannaceæ [1]), as far as descriptions go, the vascular system in the cylinder is of the Palm type; but outside the cylinder there is a system of complete cortical vascular bundles. According to Wittmack's description of Musa Ensete they are 'completely limited to the cortical layer, and have a very sinuous, almost zigzag course, especially in the lower part. Owing to their crowded arrangement and their frequent crossing, it was very rarely possible to follow their traces far. But in favourable cases it appeared that they approach rather near to the epidermis, and then proceed upwards parallel to the surface: but whenever they thus approach the base of a leaf, they curve inwards, and form anastomoses with the chief vascular bundles (bundles of the trace), till finally they themselves enter one of these leaf-bases, together with the large bundles which pass into it from the interior of the stem. They here usually turn to the outer or inner wall of the leaf-sheath, rarely they may be seen penetrating into the central regions, which are traversed for the most part by the main bundles.' Wittmack found the same arrangement in all the nine species of Musa investigated by him, in Strelitzia reginæ (weak), in the rhizome of Curcuma Zedoaria, in the flower-stalk of Phrynium violaceum, and Calathea grandiflora: Meneghini found it previously in species of Ravenala, Hedychium, and Canna.

Sect. 68. As far as hitherto investigated, the single vascular bundle of the cotyledon in the *seedling* of the Monocotyledons of the above types runs directly into the axis of the main root, e. g. Allium Cepa [2]: or the cotyledon contains several bundles, and these unite in the cotyledonary node, and then similarly pass into the bundle of the root: e. g. Palms [3]. The bundles of the leaves which follow after the cotyledons show the typical course, with such modifications as result from the small number of bundles and the shortness of the internodes to be traversed. They unite in the cotyledonary node with those of the cotyledon and of the root.

The elongated internode between the insertion of the scutellum and the first sheathing leaf in the seedling of Zea Mais shows an abnormal arrangement. It contains a ringlike mass of vascular tissue, which surrounds a wide pith: this ring is continued at the point of insertion of the scutellum into the bundle of the first root. The annular mass originates by the coalescence of the lower ends of the numerous bundles of the first foliage leaf-traces with the trace of the first sheathing-leaf. The latter contains as a rule two bundles situated right and left and in front of the median line. In the node they both bend inwards, and somewhat to the rear, and anastomose on reaching the node by means of a curved connection: they then spread out and pass down in the ring. A branch goes also from the curved connecting bundle perpendicularly downwards. The traces of the foliage-leaves consist of many bundles, and are as wide as the whole circumference of the stem: the lower ends of the lowest pass beneath the node of the sheathing-leaf between and alongside of those of the latter, and with them they form the ring. According to investigations hitherto made—which require further completion—it appears that the individual

[1] Meneghini, *l. c.*—Wittmack, Musa Ensete, Halle (Linnæa), 1867.

[2] Sachs, Botan. Zeitg. 1863, Taf. III.

[3] Mohl, Palm. Struct. p. xliv. Tab. P.—Sachs, Botan. Zeitg. 1862, Taf. IX.—Compare also the data on this point in van Tieghem, Symmetrie de Structure, &c., Ann. Sci. Nat. 5 sér. tom. XIII.

bundles of the trace cannot still be distinguished in the ring. More rarely there are in the sheathing leaf in addition to the two lateral bundles two other smaller bundles placed symmetrically in the posterior half, near to the median line of the sheathing-leaf. There was found in one case in the transverse section of the internode, in the centre of the anterior side and outside the ring, a small isolated bundle, the origin and course of which remained doubtful.

The terms anterior and posterior are in all cases to be understood here, so that the side next the scutellum is the posterior.

In conclusion, a short connected description may here be given of the peculiarities of the bundle-system in the Aroideæ and Pandanaceæ, so often alluded to above[1].

A number of forms do not differ from the Palm type, except in the fact that in many of them the bundles run for a long distance in the cortex before entering the cylinder. A second category is distinguished from the first by the bundles being united on their descending curved course within the cylinder, and at a considerable distance from its surface. In transverse sections therefore there are found within the peripheral layer 'compound' bundles, i. e. such as are cut through at the points of coalescence or separation. Finally, in a third group the bundles are not only united on their entry into the middle of the cylinder, but are connected by anastomoses in all directions, and in such a way in specially good cases that, as in the Nymphæaceæ (p. 252), there is close beneath the growing-point a complex network, which branches in all directions, and takes up the leaf-traces as they enter, so that the typical bundle system can only be recognised by slight indications.

To the *first category* belongs in the first place the rhizome of Acorus gramineus and A. Calamus: the majority of the bundles descend obliquely, as in the above-mentioned Cyperaceæ, through several internodes in the thick cortex, and this, as is especially well seen in A. gramineus, is traversed by bundles arranged in several rings in transverse sections. Further a number of epiphytic forms with elongated internodes belong here: all the Monstereæ investigated by v. Tieghem (species of Heteropsis, Monstera, Raphidophora, and Scindapsus), with bundles of the trace, which sometimes enter the leaf at once at the node, but for the most part traverse the cortex through two internodes before passing into the leaf: further the investigated species of Anthurium and Pothos, in which also cortical bundles are present, which vary in number and distribution according to the species, with the exception of A. Miquelianum, which belongs to the simple Palm type. The *second category* is connected with the above forms by the investigated species of the genus Philodendron. As in the former, some of the bundles traverse the cortex through (two) internodes before they pass out into the leaf. In Ph. micans all the bundles take an individual course through the internodes, and are only united at the nodes, the joint bundles then pass downwards, and end at the periphery of the cylinder. In other species (Ph. Rudgeanum, hastatum, tripartitum) the points of coalescence are within the cylinder in the internodes also, so that the transverse section often shows 'compound' bundles side by side with simple ones. According to v. Tieghem this arrangement is found, subject to many modifications according to the elongation of the internodes, the presence or absence of cortical bundles, &c., and specific peculiarities, in all investigated Aroideæ with moderately elongated internodes and unisexual flowers (species of Homalonema, Aglaonema, Dieffenbachia, Syngonium, and others to be named below), and of those with bisexual flowers in Calla palustris, Lasia ferox, and Spathiphyllum. To this series belong also the stems of the Pandaneæ (Pandanus javanicus, pygmæus). The thick, cylindrical (Alocasia), or almost tuberous stems, with short internodes, of other unisexual Aroideæ, Alocasia odorata, Colocasia antiquorum, Caladium esculentum, Dracunculus, Arum, Richardia aethiopica, &c. belong to the *third category*, since their bundles are not

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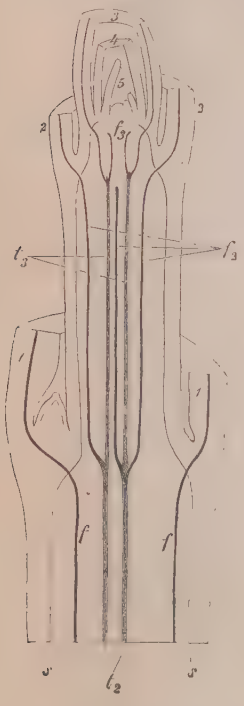
[1] See van Tieghem, *l. c.*

only frequently united within the stem, but are connected in a reticulate manner by anastomoses. Many forms, such as Syngonium, are transitional between the second group and the third. In small branches of rhizomes of Richardia æthiopica also the typical curved course may be easily recognised, especially in the ends of the branches; in Alocasia, Dracunculus, Caladium esculentum the system of vascular bundles forms 'a complicated net, in which it is impossible, by the most careful dissection of a macerated stem, to trace one bundle with certainty even for a short distance.' Still even here it may constantly be recognised, especially at the apex of the stem, how the bundles pass from the base of the leaf with a curved course to the middle of the stem, and from thence downwards and outwards.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in gardens as Tradescantia albiflora, and will be described first in that example (Figs. 119 and 120).

From the sheath-like base of the alternate distichous leaves, which embraces the stem, as a rule eight bundles curve into the node (1), and thence descend perpendicularly to the next node (2). In the internode they are at about equal distances laterally from one another, and at varying distances from the middle of the stem, but at least $\frac{1}{3}$ of the radius from it. Close above node (2) they curve towards one another and the middle of the stem, and unite in the node itself in pairs to form four bundles. These four bundles are stronger than the original eight: they are arranged crosswise near to the middle of the stem, and run perpendicularly downwards to the next node (3) where each inserts itself on the point of junction of two which pass out at node (2). Each internode accordingly shows in transverse section (Fig. 120) in the first place twelve bundles, four inner ones, arranged crosswise, and around them an irregular circle of eight weaker ones (*b*). Besides these twelve bundles of the leaf-trace there are also usually 11–12 bundles (of subsequent development) which are arranged in a circle outside the eight external bundles of the trace. This circle, together with the rather small-celled parenchyma between the bundles, marks off the *cortex* from the *cylinder* which contains the vascular bundles. Some of these bundles lie also further inwards, between the eight outer bundles of the trace. These 11–12 bundles do not pass out into the leaves, but run up into the youngest internode, passing almost perpendicularly through the internodes, curving slightly inwards at the nodes, and passing near to the outgoing bundles of the trace. Irregular short transverse bundles connect them in old nodes with one another, and with the bundles of the trace.

Deviations from the above numbers are often found, e.g. in the lower internodes of lateral shoots, where there are often in all only 18–19 bundles visible in the transverse section—e.g. 3 + 6 bundles of the trace, and 10 cauline bundles.

I found fundamentally the same arrangement both of the bundles of the trace and of the cauline bundles in all the other Commelinaceæ investigated: Commelina agraria Kth., C. procurrens Schl., Tradescantia zebrina, virginiana, Spironema fragrans, Dichorisandra thyrsiflora, D. oxypetala, Maravelia zeylanica. But in all these the number of bundles of each category is higher than in Trad. albiflora, especially in the last-named six species with a thick stem, and leaves with many bundles. The arrangement of the separate and united bundles is accordingly more complicated and requires further investigation.

Potamogeton natans (Fig. 121) has alternating leaves in two rows: these are often displaced from this arrangement (by torsion of the stem?): the leaf-trace consists of three bundles, the width of the leaf-trace is about 180°. The three bundles of the latter curve towards the middle of the stem, and pass separately down one internode, the stronger median bundle being nearer the middle line than the two lateral ones. In the next node they all three coalesce to a single bundle, which then passes down to the second node, and here inserts itself at the point of coalescence of the next lower trace (rarely one of the lateral bundles continues a separate course up to this point of insertion, Fig. 121, *x*). In the internode there appears accordingly in the bluntly rectangular transverse section (Fig. 122) of the 'cylinder' which contains the bundles, one large bundle at each end of the smaller diameter; these are opposite one another: one of these (1) is the united trace of the second higher leaf,

the other rather smaller one ($2m$) is the median bundle of the next higher leaf. At each end of the longer diameter is a small bundle ($2, 2$): these are the lateral bundles of the last-named leaf. On both sides of each lateral bundle, that is opposite each corner of the rectangular transverse section, there is further a small cauline bundle (s, s). The median bundles appear first, then the lateral ones, and the cauline bundles much later. At an early stage irregular anastomoses appear in the nodes between all of them, the small cortical bundles of sieve-tubes and fibres also taking part in these (p. 232).

Among the other Potamogetons which have been investigated, P. perfoliatus has fundamentally the same bundle-system. Also the rhizome of P. pectinatus

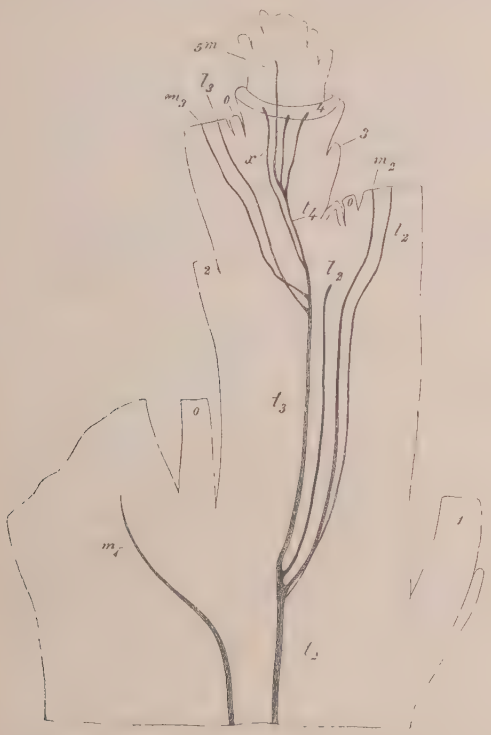

FIG. 121.—Potamogeton natans (40). End of the stem, made transparent; the outer layers of tissue removed in the lower part by longitudinal sections; successive leaves and their belongings numbered in order. m median bundle; l lateral bundles of the leaf indicated by the figures; ℓ the united portions; x a bundle of leaf 4 which runs an exceptional distance separately. The median planes of the leaves 1—3 lie alternately right and left in the plane of the paper (opposite the middle of 2 is the axillary bud belonging to it). Above 3 is a rotation, so that the median plane of leaf 4 is at the front, while that of 5 is at the back. The median bundle of 5, $5m$, therefore runs deep down into the preparation. The lateral bundles of 5 and the cauline bundles are (as yet) not visible; o = the stipular sheath of the base of the leaf.

appears, according to an incomplete investigation, to resemble it. In other species the structure resembles that described, but is simpler, and reduced in proportion to the average decrease in size of the leaves.

P. lucens and P. gramineus have a leaf-trace consisting of a single bundle, which does not divide into three bundles till its exit at the node into the leaf. Each passes

down, near to the middle of the stem, and close to that of the next lower leaf, through one internode, and then unites with the latter in the node (comp. Fig. 124). In a transverse section of the internode there are accordingly two bundles of the leaf-trace, which are close to the centre in the diameter between the median lines of the two rows of leaves. A small vertical cauline bundle appears at a later stage than the leaf-traces and near to them, and this lies in the radial longitudinal plane at right angles to the plane of the median lines of the leaves: in the nodes transverse and oblique anastomoses appear at an early stage, as in P. natans.

P. densus shows fundamentally the same structure, with the striking difference that each bundle of the leaf curves almost at right angles into the middle of the stem, and inserts itself in the next lower node directly on the bundle which there passes

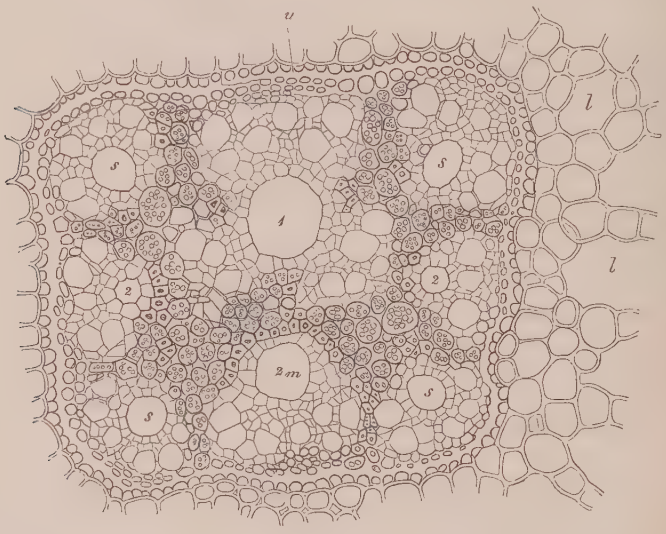

FIG. 122 (145).—Potamogeton natans. Axile body of the internode, containing the vascular bundles; transverse section. *v* endodermis thickened on one side (with starch); outside this the lacunar cortical parenchyma (with much starch); *l* air cavities. Explanation of the figures in the text. The groups of delicate tissue of the numbered areas are the phloem portions; the wide meshes in them are the sieve-tubes of the bundles; the areas in which the figures stand are their vascular portions (for the most part converted into cavities). Between the bundles is starchy parenchyma, and sclerenchymatous fibres, with a narrow lumen, which appears as a dark point.

out, so that only one axile sympodium of the leaf-trace is present besides the two cauline bundles. In the upright stems of P. pectinatus (Fig. 123), in P. pusillus and Zanichellia palustris this axile sympodium is alone present, without the two cauline bundles, to which fact we shall return later.

P. crispus shows a somewhat different arrangement, which will be described below.

It is not improbable that this type of vascular bundle-system is allied to that of Hydrocharis, Stratiotes, and their allies, but further investigations are wanted on this point.

The transverse section of the stolons of Hydrocharis Morsus Ranæ[1] shows four bundles

[1] Rohrbach, Beitr. zur Kenntniss einiger Hydrocharideen, Abhandl. d. Naturf. Ges. z. Halle, Bd. XII. p. 75.

arranged crosswise, two larger and two smaller, the similar ones being opposite one another. A few layers of cells below the epidermis a circle of eight to ten small bundles is found, which run perpendicularly and separately through the internode.

In the short thick stem of Stratiotes aloides[1] the bundles—all of which descend from the leaves—unite 'after numerous anastomoses to one central bundle and eight

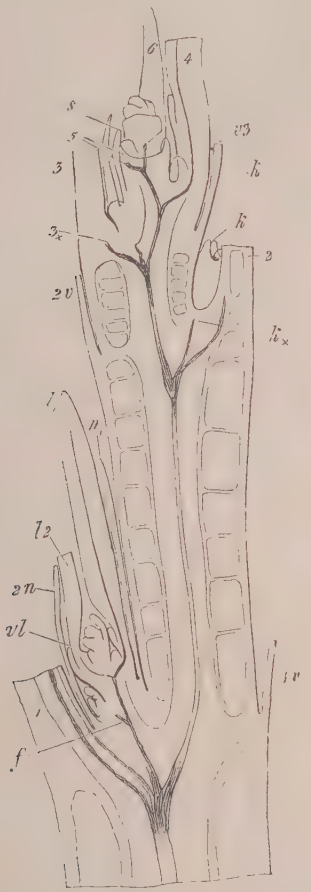

FIG. 123.—Potamogeton pectinatus; end of the shoot (40). Thick median section, cleared with potash, parallel in the lower part to the median planes of the two rows of leaves; higher up, from leaf 5 onwards, this plane has rotated through almost 90°. Successive leaves numbered successively 1—6; *v* the opposite sheathing part belonging to the correspondingly numbered leaf; *s* a *squamula intravaginalis* of leaf 3. In the middle is plainly seen the vascular portion of the sympodium of vascular bundles; the uppermost bundle, which is clearly seen, goes to leaf 6 (which lies at the back of the section); that which goes to 5 is cut transversely, since 5 was turned towards the observer, owing to the above-noted rotation. In the axils of each of the leaves (up to 5) an axillary bud is plainly seen. That belonging to leaf 2 lies deep in the section; its parts are indicated by *h*, and the vascular bundle which enters it by *h*+. That belonging to leaf 3 is still small; but the development of the first vascular bundle which enters it is beginning in the angle where the bundle 3+ (which runs into leaf 3) unites in the node with that which comes from 4. In the axil of leaf 1 is a strongly-developed axillary shoot; n_1 and n_2 its scale leaves, l_1 and l_2 its two first foliage leaves; the vascular bundle which enters l_2 is just beginning to be developed. In the axil of n_2 a secondary axillary shoot is appearing; its first vascular bundle is beginning at *f*.

or nine peripheral ones. In the thin stolons these bundles run perpendicularly through the internodes.'

[1] Rohrbach, *l. c.* p. 94.

V. Anomalous Monocotyledons.

Sect. 70. Under this term may be grouped some examples of vascular bundle-systems, which differ fundamentally from that of the very great majority of Monocotyledons. Some of these are found in certain water-plants, the rest in certain Dioscoreæ, the bundle-system of which approaches very closely to that of the Dicotyledons.

Potamogeton crispus, while it approaches very closely in other anatomical properties to other members of the genus, is distinguished from them by the course of the bundles in the stem. Comp. Figs. 124, 125.

Fig. 124.—Potamogeton crispus (40). End of a shoot. Longitudinal section parallel to the median planes of the two rows of leaves, cleared by potash. The successive leaves numbered 1, 2—10; v_1, v_2..... the sheaths of the corresponding leaves; the sheaths of the upper leaves were obscured in the process of preparation, and are partly omitted in the drawing. The median vascular bundles of leaves 9 and 10 are just beginning to develope; the seven highest leaves are still without bundles.

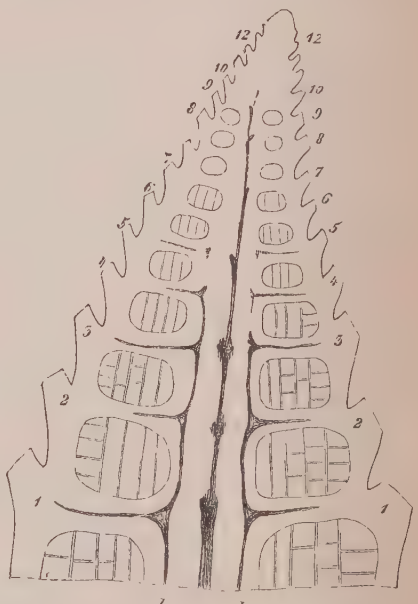

Fig. 125.—Potamogeton crispus (40). End of a shoot. Thick median longitudinal section perpendicular to the median plane of both rows of leaves, cleared by potash; the sheaths were obscured by the process of preparation, and are omitted in the drawing. The successive leaves are numbered in order. The series of unevenly numbered leaves are uppermost, nearest the observer; the even numbers are below. The same is the case with the median bundles, which go to the respective series and unite in the axile bundle *m*. The median bundle is plainly seen as far as the sixth leaf from the apex; the lateral bundles united to form the two bundles *l*, *l*, beginning at the eleventh leaf from the apex (5) in the node; the development of 4 and 5 is not yet completed downwards through the internode. In the internodes the air-cavities are first formed from below upwards, and from the outside inwards.

In each of the sheathing leaves, which alternate in two rows, the bundles pass out at the node. The median bundles run down through the internodes in the manner described for P. lucens and gramineus (Fig. 124). The lateral ones (Fig. 125) pass on each side almost perpendicularly from a bundle which traverses the stem perpendicularly, and corresponds exactly in position and relatively late appearance to the cauline bundles of the other species, so that the arrangement of the

bundles in a transverse section of the internode is the same as in them. The lateral bundles of the stem of P. crispus are however not cauline. The development of their tracheæ begins at the nodes, and proceeds from each of these towards the middle of the next upper and lower internodes (Fig. 125, 4, 5).

The course of the three bundles in the stem of Zostera marina[1] is just the same as the above: one axile bundle is built up sympodially from the median bundles of the leaves, while two lateral ones, which lie in a plane cutting the median-plane of the bi-seriate leaves at right angles, give off lateral bundles to the leaves; these however require further investigation. The arrangement of the bundles in the transverse section of the internode of Zostera differs from that in Potamogeton, since in the latter the lateral bundles are close to the central bundle, while in the former they run at some distance from it, near to the surface of the stem.

In Cymodocea æquorea Koen.[2] the median bundle of the seven bundles of the trace runs obliquely down to the middle of the stem, it there passes perpendicularly to the next node, where it joins the median bundle, which there passes out. The transverse section of each internode thus shows a central bundle. Near to the periphery of the stem 20–25 small bundles (in weak stems fewer) arranged in two concentric circles pass perpendicularly through each internode. Each of these, according to Bornet, divides at the node into two, of which one ascends into the next higher internode, the other either curves out into the leaf, or unites either with a neighbouring peripheral bundle, or with the axile bundle. Besides this a complex network of anastomosing bundles is formed in the node between the different bundles. The peripheral ones appear to be cauline, but this requires to be further investigated. As far as may be judged from transverse sections Cymodocea isoetifolia exactly resembles other species.

After what has been said it need not be stated in detail how Hydrocharis and Stratiotes might, as far as our present knowledge goes, belong equally well to this as to the preceding section: this will have to be decided by further investigation.

Sect. 71. In the foliage-shoots of Tamus and Dioscorea Batatas the vascular bundles are arranged according to the Dicotyledonous type, that is in a ring surrounding the pith. It is true that here the bundles pass an unequal distance into the pith, but this also occurs in typical Dicotyledons.

Nägeli (*l. c.* p. 123) gives the following description of Dioscorea Batatas. The leaves are sometimes spirally arranged, sometimes in decussating pairs. The leaf-trace consists of three bundles. When the arrangement is decussate (Figs. 126, 127) its width is about 120°. If their course in a tangential direction be first considered (Fig. 126), the six bundles of one pair of leaves pass nearly straight down two internodes, the lateral bundles (*bc*, *ef*; *hi*, *lm*; *op*, *rs*; *uv*, *yz*) pectinating at the first internode with the lateral ones which there enter. Above the bundles of the second lower node the two lateral bundles of one trace converge towards one another, and insert themselves on lateral bundles of the next lower pair; but the median bundle (*a*, *d*; *k*, *g*; *t*, *x*) divides into two shanks which unite with the same

[1] Compare Magnus, Botan. Zeitg. 1872, p. 216.

[2] Bornet, Recherches sur le Phucagrostis major, Ann. Sci. Nat. 5 sér. tom. I. Compare especially p. 39, pl. 6. fig. 1, and pl. 11, fig. 1.

lateral bundles. The leaf-trace is here much contracted, and usually forms by coalescence one single mass. The six bundles of one pair of leaves thus go through only two internodes before they coalesce with lower ones, and the transverse section through an internode shows twelve bundles (Fig. 127), of which six pass out at the next node and six at the node above it. These twelve bundles would be arranged in a circle if they had a radially perpendicular course. But this is not the case: they penetrate further into the pith as they pass down lower. Their radially oblique course is however restricted almost entirely to the nodes: the same bundle thus appears at unequal distances from the centre in the two internodes. The lateral bundles, which in their first internode are nearer the centre than the median ones, differ still more from them in this respect in the next lower internode. The transverse section through an

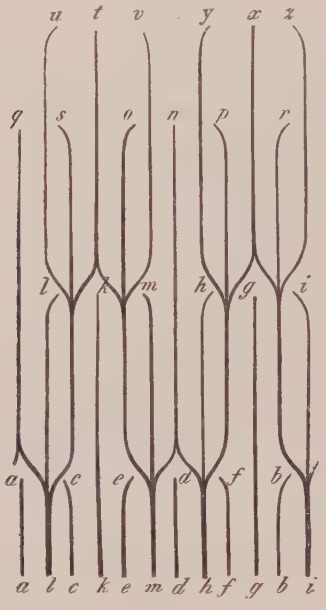

Fig. 126.

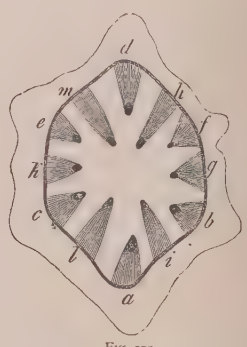

Fig. 127.

FIGS. 126, 127.—Dioscorea Batatas, with decussating pairs of leaves; after Nägeli. Fig. 126. Scheme of the vascular bundle-system in the end of a shoot, the cylindrical surface being reduced to a single plane. Fig. 127. Transverse section through an internode, the same bundles being indicated by the same letters as at the bottom of Fig. 27; further explanation in the text.

internode therefore shows four bundles which project further inwards and form a rectangle,—these are the lateral bundles of the next higher pair of leaves,—and eight outer bundles.

On the longitudinal course where the leaves in Dioscorea are arranged spirally, and on Tamus, compare Nägeli, *l. c.*

The course of the bundles in Monocotyledonous stems has recently been the subject of extended researches by Falkenberg[1]. The chief result of that work which

[1] P. Falkenberg, Vergl. Untersuchungen über den Bau der Vegetationsorgane der Monocotyledonen, Stuttg. 1876.

concerns us here was briefly stated in 1874[1]: it is the discovery of a new form of bundle system in the *foliage-* or flowering-stems of Lilium, Tulipa, Fritillaria, Cephalanthera, Epipactis, and Hedychium. The course of the bundles is such that the bundles of the leaf-trace penetrate downwards, and for different distances inwards towards the middle of the stem, and then affix themselves on corresponding bundles of lower leaves, *without having previously curved outwards*. For the rest we may here refer to Falkenberg's comprehensive work, and print off the above paragraphs without alteration as they were written down about four years ago, since they coincide in the main with his work.

VI. Phanerogams with an Axile Bundle.

Sect. 72. A number of plants with reduced foliage and roots living in water or marshes, and some in damp humus, belonging partly to the Monocotyledons, partly to the Dicotyledons, show the bundle-system of the stem united into one bundle, which is surrounded by a thick cortex, and traverses the middle of the stem longitudinally: from it bundles pass at the nodes into the leaves. With this simplicity of course there is usually connected a considerable simplification in the structure of the bundles, which always shows peculiarities: we shall return to them in Sects. 105 and 110.

As regards the coarser structure, and especially the relations to the bundles of the leaf-trace, which it may be said require more exact study in many cases, there may be distinguished two chief forms. Firstly, axile bundles, formed or developed sympodially from weak bundles of the trace, which approach closely to one another, and coalesce longitudinally: thus they do not differ in their first origin from the typical bundle-systems of the Phanerogams: secondly, such as are cauline, and grow acropetally with the end of the stem; the bundles which run to the leaves are given off from the former at the nodes, or apply themselves to them as branches: thirdly, those cases in which the axile bundle is built up of longitudinally coalescent bundles of the leaf-trace together with cauline bundles are connected with the two former cases as intermediate forms.

To the first category belong the following Dicotyledons: Bulliarda aquatica according to Caspary's account[2], Hottonia, Elatine Hydropiper, hexandra, also E. Alsinastrum[3], and probably Trapa natans: of Monocotyledons, Potamogeton pectinatus and pusillus, to which may be added Zanichellia[4] and Althenia[5]; also Ruppia[6] and its allies. To the second category the following Dicotyledons belong: Aldrovandia[7],

[1] Botan. Zeitg. 1874, p. 732.

[2] Schriften d. Physical. öconom. Gesell. zu Königsberg, Bd. I. 1860.

[3] [Comp. Friedrich Müller, Struktur einiger Arten von Elatine, Flora, 1877, p. 481.]

[4] Schleiden, Beitr. p. 215.—Caspary, Pringsheim's Jahrb. pp. 383, 440.

[5] Prillieux, Ann. Sci. Nat. 5 sér. tom. II.

[6] Compare Irmisch, Ueber einige Arten d. Familie d. Potameen (Abhandl. d. Naturwiss. Vereins f. Sachsen und Thüringen, 1858), p. 44.

[7] Caspary, Botan. Zeitg. 1859, p. 126, Taf. V. Ibid. 1862, p. 193.

Hippuris[1], Callitriche[2], Myriophyllum[3], Ceratophyllum[4], probably Utricularia, and the non-aquatic genus of Piperaceæ Verhuellia[5]: of Monocotyledons, the Hydrilleæ, Elodea canadensis, and Hydrilla verticillata[6]; Najas[7], and the rhizomes of the rootless Orchids which grow in humus, Epipogon Gmelini, and Corallorrhiza innata[8]. In Corallorrhiza and the stolons of Epipogon a branch passes from the axile bundle into each of the biseriate scale-leaves: in the coral-like rhizome of Epipogon, which has short internodes, the branches which pass to the leaves are absent, according to Reinke.

According to the structure and development of the bundle the following plants may be placed in the third intermediate category; perhaps Myriophyllum, Hippuris, and Elatine Alsinastrum: further the larger Potamogetons belong to this series: their original arrangement of cauline bundles and bundles of the trace has been described above on p. 272. In the series of described species of this genus, and of allied forms such as Zannichellia and Althenia, with which Elodea, Najas, &c. are also connected, there are to be found all stages of simplification of composition (and of structure) of the axile bundle: leaf-traces consisting of one or more bundles, running side by side with cauline bundles through the internodes, are found in the stronger, more leafy forms, at one end of the series, while at the other a single cauline bundle is present, which unites at the node with the bundles from the leaves.

VII. Fern-like Plants.

Sect. 73. In the young seedlings of all the investigated forms of this series the bundle-system of the stem is a sympodium of leaf-traces consisting of one bundle (which with the exception of Equisetum developes in an acropetal direction). The first bundle, which usually ends blind in the foot of the embryo, curves after a very short course through the stem into the first leaf; from the point of curvature the development of a bundle, which runs out into the second leaf, begins. In the case of the subsequent leaves the same conditions prevail.

In Isoetes, Equisetum, and Osmundaceæ, this construction of the bundle-system out of distinct leaf-traces is permanent even in the mature stem. The same holds perhaps for many Ferns with a simple axile bundle. In the Lycopodiums, and Selaginellas, the axile bundle which traverses the stem, or the two or more bundles

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[1] Nägeli, Beitr. *l. c.* p. 56.—Sanio, Botan. Zeitg. 1865, p. 191.

[2] Nägeli, *l. c.*—Hegelmaier, Monogr. d. Gattung Callitriche. Idem in Martius, Flora Brasil. fasc. 67.

[3] Vöchting, Zur Histologie u. Entwicklungsgeschichte v. Myriophyllum, Acta Acad. Leopold. XXXVI (1872).

[4] Schleiden, Beitr. p. 216.—Unger, Anatom. und Physiol. 198.—Sanio, Botan. Zeitg. 1865, p. 192.

[5] Schmitz, Flora, 1872.

[6] Caspary, in Pringsheim's Jahrb. I. Idem, Verhandl. d. Naturforscher u. Aerzte z. Königsberg, 1860.

[7] Compare Magnus, Beitr. z. Kenntniss d. Gattg. Najas, p. 48.

[8] Irmisch, Beitr. z. Morphologie und Biologie d. Orchideen.—Schacht, Pflanzenzelle, p. 268. Idem, Lehrbuch, II. p. 21.—Reinke, in Flora, 1873.

of many Selaginellas, may, as regards development, be considered as a cauline bundle, the corners of which are composed of the sympodially united leaf-traces of a single bundle. On the other hand, the Lycopodiaceous plant, Psilotum triquetrum, has only a cauline bundle without leaf-traces. Also in the case of Marsilia and Pilularia a similar view may be held, in common with Nägeli, according to the development of the bundles. In the majority of the Ferns there is an obvious connection between the form and arrangement of the leaves, and of the bundles which enter them; in a number of cases, especially in those forms, to be described later, with a reticulate stem-system, and one bundle for each leaf, the stem-system may be recognised as being composed of the constituent leaf-traces[1]. But in very many cases such a separation cannot be carried out according to our present knowledge without arbitrary treatment, but rather a bundle-system of varying form and complication may be distinguished in the stem, from which bundles for the leaves are given off at certain points. The following description must accommodate itself to the facts: in each case those stem-systems, which may arbitrarily be recognised as being composed of leaf-traces, will be associated with those with which they correspond most closely in their real structure.

There may accordingly be distinguished on the one hand the types of Equisetum, Osmunda, Isoetes, on the other the various series of types of the Ferns, which are connected by numerous intermediate forms: under the latter the Lycopodiums and Selaginellas may be ranged as peculiar instances, and are here co-ordinated merely for synoptical reasons.

Sect. 74. **Equisetum**[2]. The weak bundles of the stem are arranged in a ring separating the pith and cortex. From the median line of each tooth of the leaf-sheath one bundle enters the stem, it here passes perpendicularly down one internode, and then divides, at the next lower node, into two short shanks, each of which affixes itself on the nearest lateral bundle which here passes out. Where the number of teeth of successive sheaths is the same the bundles of successive internodes alternate as they do.

Sect. 75. **Osmundaceæ**[3]. Comp. Figs. 128–130. The mature rhizome of Osmunda regalis has leaf-insertions arranged with a divergence of $\frac{5}{13}$, and short internodes. Its centre is occupied by an irregular bluntly five-cornered prism, with a thickness of about 6^{mm} in strong specimens: this consists of a vascular-bundle-cylinder (Ring), a narrow sheath of delicate-celled parenchyma surrounding the latter, and a parenchymatous pith surrounded by the ring of bundles, and with brown sclerenchymatous cells scattered through it. The prism is enclosed by a cortex 2–5^{mm} in thickness, which is dark-brown and sclerotic, but contains much starch: this is traversed by vascular bundles, also surrounded by a thin sheath of delicate parenchyma, on their oblique upward course from the ring into the leaves (Fig. 128).

[1] See Holle, Botan. Zeitg. 1875, p. 265, &c.

[2] Nägeli, Zeitsch. f. wiss. Bot. 3. p. 143; Beitr. *l.c.* p. 57.—Cramer, in Nägeli und Cramer, Pflanzenphys. Unters. Heft 3, p. 21.—Hofmeister, Vergl. Unters. p. 93.—Duval-Jouve, Hist. Nat. des Equisetum de France, 1864.

[3] Göppert, Flora, 1848, Taf. IV. A.—Unger, Denkschr. d. Wiener Academie, Math.-Naturwiss. Classe, Bd. VI (1853).—Milde, Monogr. Osmundæ, p. 32.

One bundle enters each leaf: the arrangement of the bundles in the cylinder is quite similar to that of the Coniferæ with alternating leaves with a single bundle (Fig. 130). From one leaf *n* one bundle enters the cylinder, and runs almost perpendicularly downwards, as a rule through 13 internodes, and then, when close to the leaf *n*–13 perpendicularly below it, it curves towards the ascending side of the bundle belonging to the leaf *n*–8, and unites with it. In the cases investigated the insertion and coalescence took place occasionally even after a shorter course, e. g. in the case of the bundle 10 in Fig. 130, eight internodes below the point of exit. The bundles are strongest at their point of exit from the cylinder, and are of horseshoe shape. In the petiole they retain this form, or are at least half-moon-shaped. In the cylinder of the stem, as they pass downwards, they decrease in thickness at first gradually, and then quickly, and assume a wedge-shaped transverse section. Here they are separated from one another by narrow bands of parenchyma (medullary rays). The structure of the whole transverse section (Fig. 128) may be deduced from the above description.—The bundles, which pass into the first leaves of the seedling, unite to an axile bundle without any pith: this gradually extends into the ring of bundles surrounding the pith.

Fig. 128.

Fig. 129.

FIGS. 128 and 129.—Osmunda regalis. Fig. 128. Transverse section through a strong stem, seen from above, i. e. from the apex of the stem; magnified about twice. *i* lowest bundle of leaf-trace, from which a root-bundle passes through the cortex.

Fig. 129.—Sketch of the bundle-ring in the former figure, more strongly magnified. 1. Bundle of the lowest trace cut through just at its point of entry into the ring, and with one of the two root-bundles, which are here attached to it. The figures 1—13 indicate the bundles of the trace of the thirteen successive leaves, which are visible in the transverse section; No. 10 is abnormally united with 2 Compare Fig. 130.

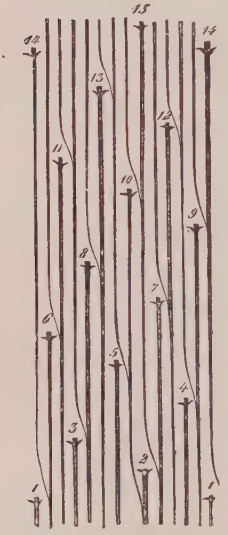

FIG. 130.—Osmunda regalis. Scheme of the vascular system in the stem, the cylindrical surface being reduced to a single plane; arrangement of the leaves 5/13. The bundles of the leaves numbered in genetic series at their point of exit; each has two roots inserted close to the point of exit, and indicated by short transverse strokes. On 2 and 10 is to be seen the anomaly observed in the specimen upon which the scheme is founded, viz. that 10 inserts itself on 2 close to the point of exit of the latter, instead of continuing its course to 2—5.

In Todea africana and T. hymenophylloides are seen phenomena exactly similar to those in Osmunda, which need not be described in detail here.

SECT. 76. While thus the bundle-system of these plants, and of the Equiseta, may well be ranged under the type of Dicotyledons, and is specially allied to that of the Conifers (Juniperus, Widdringtonia[1]), the species of **Isoetes** have in their extremely shortened tuberous stem an axile bundle without pith, as is the rule in submerged water-plants: this bundle is built up sympodially by the coalescence of the inner ends of the one-bundled leaf-traces. Phylloglossum may also belong to this category[2].

SECT. 77. **Psilotum** and **Lycopodium**. The leafy stem of Psilotum triquetrum[3] has one vascular bundle with 2–8 corners which project more or less from the surface. It is cauline throughout, the small leaves have no vascular

[1] Compare above, p. 246, and Geyler, *l. c.*, especially Taf. IV.

[2] Compare Mettenius, Botan. Zeitg. 1867, p. 98.

[3] Nägeli, Beitr. *l. c.* p. 52.

bundles. Still, according to Nägeli there is a relation between the corners of the bundle and the insertions of the leaves. 'At some distance (about 3–8^{mm}) perpendicularly below each leaf one corner of the bundle projects very strongly, and gradually loses itself below, but rather more quickly above. The corners of the bundle are therefore the more numerous in a portion of a stem, as the vertical rows are more numerous of the otherwise irregularly arranged leaves, which can only with difficulty be referred to a cyclic arrangement.'

The leaves of the *Lycopodia*[1] are arranged, according to the species and individual, in alternating whorls of two or more members, or spirally with a divergence of $\frac{2}{9}$, $\frac{2}{11}$, $\frac{2}{13}$, &c. Each contains one thin vascular bundle. The stem is traversed by one strong, almost cylindrical axile bundle, in which the symmetrically distributed bands of tracheides, to be described in Sect. 107, form external protrusions, which, like the bundles passing into the leaves, and the above-mentioned corners in Psilotum, consist of narrow spiral tracheides, and may like them be briefly termed corners. The bundles of the leaves insert themselves (when followed from the base of the leaf) after a curved downward course through the cortex, on the corners of the axile bundle. At the beginning of the differentiation of tissues, there is at first a bundle of spiral tracheides at the corner, which forms a direct continuation of that which passes into the leaf: it passes down through some internodes, and then inserts itself on the point of curvature of one which passes out lower down. It is only later that the more internal masses of larger tracheides are developed.

From these facts, and according to the phenomena of development, the axile cylinder may be characterised as a cauline bundle, on the corners of which the sympodially united bundles of the leaf-trace are directly inserted. The same facts, however, admit equally well of our speaking of a polyarch (Sect. 107) axile bundle, which gives off branches from its corners into the leaves.

The origination of the bundle which passes into the leaf follows very soon after the protrusion of the young leaf itself. The development of each bundle of spiral tracheides begins where the bundle inserts itself upon the point of curvature of a lower one, and proceeds towards the apex of the leaf in question: then from the point of curvature it proceeds again in the same direction to a higher leaf. This happens very rapidly, at least in the stem itself, so that only in favourable cases (in L. alpinum) could Hegelmaier find a bundle of spiral tracheides, of which the portion passing through the cortex to the leaf was not already equally developed with the lower part, which passes down the corner; and Cramer ascribed to L. Selago a simultaneous development of the whole bundle from its lower point of insertion to the apex of the leaf—while Hegelmaier found a basipetal direction of development in the leaf itself.

The corners of the axile bundle, as also the rows of leaves, differ greatly in number in different species, individuals, and shoots of different rank of one individual, and correspond to one another as a rule neither in number nor arrangement in one and the same shoot, while apparently the correspondence is less close the greater the number of both. It is true Hegelmaier found a correspondence of both in 75 per cent. of the last branchings of L. alpinum which are covered by four rows of leaves in decussating pairs, and in about 60 per cent. of the branches of L. complanatum. But in most cases the number of

[1] Nägeli, Zeitschr. f. wiss. Bot. Heft 3 and 4, p. 132.—Cramer, in Nägeli und Cramer, Beitr. Heft 3.—Hegelmaier, Botan. Zeitg. 1872, p. 789, &c.—Sachs, Textbook, 2nd Eng. Ed. p. 468.

corners is smaller than that of the rows of leaves: in L. Selago, e.g. with whorls of five members (that is ten rows), there are 4–6, in L. inundatum with $\frac{2}{5}$ arrangement of the leaves 4 or 5, in the above-mentioned branches of L. alpinum 3, &c. From Hegelmaier's statement that in the main vegetative axes of L. clavatum and L. annotinum, with a divergence of $\frac{2}{9}$, $\frac{2}{11}$, $\frac{2}{13}$, there were found 10–17 corners, it would appear that there is a higher number of corners than of rows of leaves.

Where the rows of leaves correspond exactly to the corners, all the bundles of one row of leaves insert themselves on the same corner. In other cases one corner may take up bundles from one row only, but must also often take them from more than one row. Usually it only takes up the bundles of two neighbouring rows, but sometimes also single bundles of more distant rows[1]. The bundles insert their inner end irregularly, sometimes on the right, sometimes on the left, and sometimes on the inner side of the next lower bundle.

Sect. 78. **Selaginella**. A number of species, forming no doubt the majority, such as S. Martensii, S. helvetica, pubescens, rupestris, &c., have in each shoot one axile, ribband- or plate-like vascular bundle, the faces of which in relation to the ground are directed upwards and downwards, while the margins are lateral to the right and left: in some, as S. pubescens, the bundle is provided at the middle line of its under surface, and near to each lateral margin with a sharp band-like process. The leaves have each one small bundle, and these behave in their course and insertion one on another, and also on the cauline portion, similarly to the leaf-bundles of Lycopodium. They are inserted on the bundle at its margins: in the species with two double rows of leaves, one facing towards each side, the bundles of the two corresponding rows (that is those from one row of upper and one of lower leaves) insert themselves on each lateral margin: in S. rupestris with leaves in many rows, the bundles of several rows pass to each margin. S. Kraussiana, Galeottii[2], and most other articulatæ[3] have, instead of one axile bundle, two which run near the middle line, each following one double row of leaves: each takes up the leaf-bundles on its own side, viz. those from one upper and one lower row of leaves, at its outer margin, with the same arrangement, as in the first-mentioned series of cases.

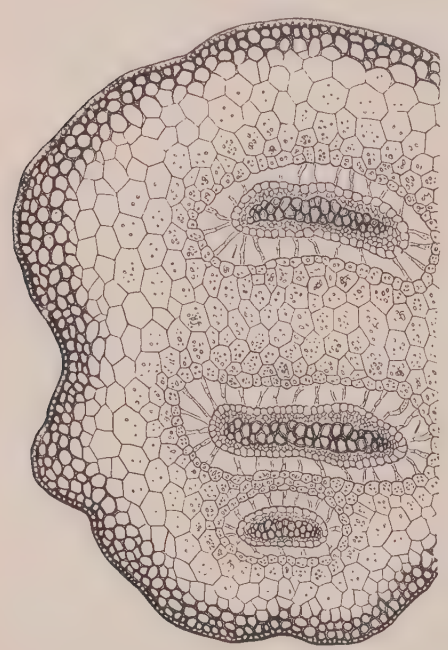

Fig. 131.—Selaginella inæqualifolia; transverse section of the stem (150). From Sachs' Textbook.

[1] Compare Cramer, *l.c.* p. 14, Taf. 30, 31.
[2] Nägeli, Beitr. *l.c.* p. 53.—Hofmeister, Vergl. Unters.
[3] A. Braun, Monatsbr. d. Berliner Academie, 27 Apr. 1865.

Other species of the genus show a different arrangement of the bundles in the stem, such as '2 median, 3 median, 3 forming a triangle, or numerous scattered bundles[1].' S. inæqualifolia shows three median ones (Fig. 131). S. Lyallii has in its strong main shoots, which emerge above the ground, ten or twelve bundles distributed in the transverse section in three parallel equidistant rows in an almost quadratic surface; where the number is ten they are so arranged that three roundish ones form two opposite sides of the quadrangle, while one transversely extended one occupies each of the two other sides, and two other roundish ones lie in the middle of the quadrangle and form, with the two transversely extended ones, a row of four parallel to the rows of three. Other transverse sections of the same shoot show in place of one of the transversely extended bundles two contiguous round ones, which are doubtless products of its division. The course of the bundles and the insertion of the bundles of the leaves have not as yet been investigated in those shoots which have other than one axile bundle or two lateral ones. In S. spinulosa, which has homomorphous leaves in many rows, there is a single axile bundle of roundish transverse section (and with a structure differing from that of other species): the leaf-bundles insert themselves on it on all sides.

Filices and Hydropterideæ[2].

Sect. 79. It has been already stated that there is always in the seedling of these plants one axile bundle composed of the single, acropetally developed bundles of the leaves. In many cases each lateral shoot begins with one such bundle.

In a number of forms this structure is persistent in the mature stem. In the large majority the bundle extends itself, and forms a tube, which surrounds a parenchymatous cylinder of pith, and is enclosed in a parenchymatous cortex. At the insertion of each leaf the tube has a gap, the *foliar gap*, from the margin of which the bundles start, which go into the leaf; at other points it is closed, or reticulately perforated. Of this *simple bundle-tube*—or ring of bundles as it appears in transverse section—several special forms may be distinguished.

In relatively few cases there are in addition to the simple tube *accessory, medullary, and cortical bundles*, or there appear *several concentric* tubes or rings.

a. Axile bundle and simple bundle-tube.

Sect. 80. *One axile bundle*, from which a branch goes to each leaf, traverses, as in submerged Phanerogams, the floating stem of Salvinia and Azolla. It occurs also in the rhizomes of Pilularia minuta, exceptionally also in weak plants of P. globulifera[3], in the investigated stems of species of Hymenophyllum[4], Gleichenia,

[1] Compare A. Braun, *l. c.*

[2] Mohl, Structura caudicis filicum arborearum, &c. in Martius, Ic. Plantar. crypt. Brasil. Tab. 29-36 —Verm. Schriften, p. 108.—Hofmeister, Beitr. zur Kenntniss d. Gefässkryptogamen, II.—Abhandl. d. K. Sächs Gesellsch. d. Wissenschaften, V. p. 602.—Stenzel, Ueber d. Bau u. d. Wachsthum d. Farne, Nova Acta Acad. Leopold. Bd. 28.—Mettenius, Ueber den Bau von Angiopteris, Abhandl. d. K. Sächs Gesellsch. d. Wissensch. IX. p. 500.—Trécul, Ann. Sci. Nat. 5 sér. tom. X. p. 344, and tom. XII. p. 218.

[3] Russow, Vergl. Unters. p. 13.

[4] Mettenius, Hymenophylleæ, *l. c.* (compare above, p. 126).

Lygodium[1], and also of Schizæa, and the leafless stolons of Nephrolepis. The bundle has usually a circular transverse section, in Salvinia rotundifolia it is horse-shoe-shaped.

Sect. 81. In many Ferns the original axile bundle widens out as the stem grows stronger into a tube, which is for the most part closed all round, and has only at each node, below the insertion of the leaf, a relatively small slit or *foliar gap*, through which the medullary parenchyma is connected with the cortex, and from the margin of which one or several bundles pass into the leaf. To this series belong for the most part forms with a thin creeping rhizome, and leaves alternating in two rows: the investigated species of Marsilia, normal specimens of Pilularia globulifera[2] with a very small foliar gap, from the lower margin of which a foliar bundle arises. Most species of Dennstaedtia (D. tenera, scandens, davallioides, punctilobula) have a tube, which is closed as far as the foliar gap; the bundle which enters the leaf arises from the whole margin of the gap as a continuous concave plate, which is only occasionally split up at its base for a certain distance into several bundles lying side by side. 'The same structure is found in all species of Microlepia and Hypolepis, in the species of Phegopteris, which are allied to the latter genus, and in the species of Pteris of the section P. vespertilio, aurita;' further in Polypodium Wallichii, and conjugatum, to the bundle-tube of which attention was first drawn by R. Brown, and in which a bundle passes into the leaf from each side of the narrow slit-like foliar gap[3]. Of the Hymenophyllaceæ, Loxsoma has a closed tubular bundle[4], the foliar gaps of which have not been described. Of the Schizæaceæ[5] the species of Schizæa may perhaps be mentioned here: but for reasons which will be given below (Sect. 106) Russow has correctly placed them in our previous category: otherwise they have been as yet but little investigated. Among the Ophioglossaceæ the above described structure occurs in the rhizome of Botrychium Lunaria[6]. Hofmeister[7] found in Ophioglossum vulgatum the network of bundles of the rhizome, which belongs to the next category, sometimes coalescent for a certain distance to form a closed tube.

Sect. 82. Most Ferns with an ascending or upright rhizome or stem, with leaves in many rows, and but slightly elongated internodes, are distinguished fundamentally from the type just described in this point only, viz. that the foliar gaps are relatively large, and the bands of the bundle-tube, which separate them, are relatively narrow. The tube has accordingly the form of a *Net*, the meshes of which are the foliar gaps. From the margins of the meshes branch the foliar bundles, which there run obliquely upwards through the cortex to the insertion of the leaf. The bundles of the meshes of the stem are, according to the species, relatively narrow, of round or elliptical transverse section, or, as in stems of the Cyatheaceæ, broad, or band-shaped plates, with their margins often curved outwards: the bundles which pass into the leaf show the same varieties of form: their number for each leaf is constant within narrow limits in the mature plant of each species, but varies in different species

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[1] Russow, *l. c.* [2] Russow, *l. c.* [3] Mettenius, Angiopteris, p. 544.
[4] Mettenius, Hymenophyllaceæ, p. 418.
[5] [Comp. Prantl, Morphologie d. Gefässkryptogamen, Heft 2, Leipzig, 1881.]
[6] Russow, *l. c.* p. 117, &c. [7] Beitr. III. p. 664.

from one to very high figures. Where several bundles pass out, they often anastomose with one another in a reticulate manner immediately after leaving the foliar gap: this is especially the case in the Cyatheaceæ. From the various combinations of these different relations result the most various individual forms of the net and of the grouping of the bundles in the transverse section of the stem: a cylindrical pith is always surrounded by them.

To this type belong numerous Polypodiaceæ, a number of the Cyatheaceæ, of the Schizæaceæ, Aneimia, of Ophioglossaceæ, Ophioglossum (O. vulgatum, O. pedunculosum). Peculiarities may be subsequently described in a few examples.

The seedling of Aspidium Filix mas begins with leaves arranged with $\frac{1}{2}$ divergence: their solitary bundles are united sympodially in the stem to one axile bundle. Above the 5th–6th leaf the stem increases greatly in thickness, the $\frac{1}{3}$ arrangement passes over to $\frac{3}{8}$, and from the point of outward curvature of the bundle of the highest leaf of the $\frac{1}{3}$ arrangement the formation of the reticulate bundle-tube begins. Each leaf receives one bundle from the lower angle of the rhombic mesh or foliar gap, upon which its base is seated: or, in other words, two bundles run into each leaf, arising from the point of exit of those which pass into the two next lateral older leaves: these converge acutely towards their own point of exit, and are there united into a single bundle. By the repetition of this formation the network of rhombic meshes is built up. Where the arrangement is $\frac{3}{8}$ there pass up to leaf 9 one bundle from 6 and one from 7, to leaf 7 one from 4 and one from 5, &c. In the second year the plant becomes much stronger, the leaf arrangement passes over to $\frac{5}{13}$, which divergence is retained in the mature plant, or passes over into $\frac{8}{21}$[1].

Each leaf now receives several bundles from the margin of its foliar gap, at first five, in mature and strong stocks seven: one arising from the lower angle, and six from the sides of the mesh; of the latter two weaker ones on each side, belonging to the lower half of the mesh, and one stronger one belonging to the upper half[2]. The structure of the meshes is the same with $\frac{5}{13}$ arrangement as with $\frac{3}{8}$; at the lower angle of each, where the median bundle passes into the leaf, two bundles which descend from the centre of the two next lateral older leaves come into contact—that from the one side following the parastichies composed of every third leaf, that from the other the parastichies composed of every fifth leaf (comp. Fig. 132). The transverse section of the mature stem thus cuts eight vascular bundles (where the arrangement is $\frac{8}{21}$, 10–12 bundles), which form a circle round a wide pith: outside this in the cortex are seen the bundles which pass obliquely into the base of the leaf, arranged in different number and order according to the position of the section. The vascular bundles of the stem are weak compared to the mass of the parenchyma, in transverse section they are roundish or flattened externally and internally (Fig. 133).

According to the numerous investigations of Hofmeister, Stenzel, and Mettenius, fundamentally the same structure—even the narrow, reticulate bundles, which are weak in arborescent stems—is found in Onoclea, Struthiopteris, in all investigated species of Blechnum (incl. Lomaria), Woodwardia, Asplenium, Phegopteris, species of Aspidium with a stem having leaves in more than two rows, in Ophioglossum, and Aneimia. The individual peculiarities depend partly upon the form of the meshes corresponding to the elongation of the internodes—thus very elongated meshes are found in the runner-like branches of the rhizome of Struthiopteris, Aspidium cristatum, in the creeping stems of A. Thelypteris, quite short and broad ones in Aspl. Filix fœmina—partly upon the number and arrangement of the leaf-bundles which arise from the margin of a gap. Most

[1] A. Braun, Schuppen d. Tannenzapfen, Nova Acta Leop. vol. XV. p. 278.

[2] Hofmeister, Beiträge II.—Stenzel, *l. c.*

of the investigated species of Aspidium have according to Stenzel's account three or five bundles for each leaf, one median, one from the lower angle, the others arising in pairs from the sides of the mesh: in Aspidium Thelypteris the median one is absent, according to Stenzel (Tab. V. 18), one bundle passing into the leaf from each side at the middle of the very elongated mesh. Blechnum Spicant (Stenzel, Tab. II. 5) has two lateral ones, one arising on each side, close to the lower angle of the mesh, Bl. brasiliense however has seven, one median and three pairs of lateral ones, arising from the lower half of the mesh. In Asplenium Filix femina, the mature rhizome of Struthiopteris [1], in Aneimia, and Ophioglossum the same arrangement is found, which appears only in the young plant of Filix mas, viz. each leaf receives only one median bundle from the lower angle of its gap. It is remarkable, according to Stenzel's account (*l.c.* Tab. II. 3), that in the scale leaves of the elongated runners of Struthiopteris the median bundle is absent, and in its place a bundle runs on each side from the middle of the long mesh.

Among the Cyatheaceæ, Dicksonia (Balantium) antarctica, Karsteniana, Cibotium Schiedei, glaucescens, Plagiogyria biserrata, Alsophilia pruinata, blechnoides [2], have—in contradistinction to their nearest allies to be described below—the same structure as is now under discussion. The appearance of the transverse section of most of these plants, which differs so strikingly from that of the Polypodiaceæ, depends partly upon the form

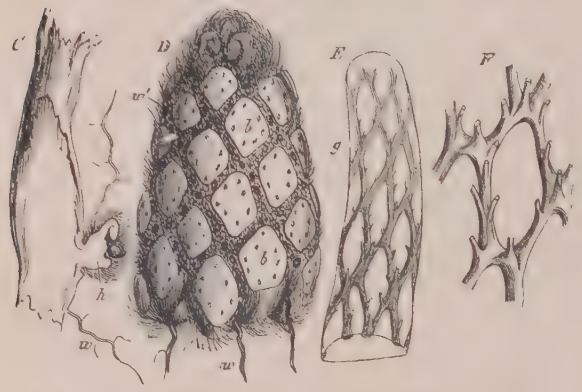

FIG. 132.—Aspidium Filix mas; natural size. *F* slightly magnified; *D* end of the stem, the leaves of which are cut off, excepting the highest ones; *b* transverse section of a petiole; *w* roots; *E* a similar end of a stem, the network of bundles exposed by paring off the cortex (*g*); *F* mesh of the net, with insertions of the foliar bundles; *C* base of the petiole, with a lateral bud *h*, longitudinal section; *w* root. From Sachs' Textbook.

FIG. 133.—Aspidium Filix mas; transverse section through a strong stem, with 8/21 leaf-arrangement; natural size.

of the vascular bundles in the stem itself, these being broad plates, usually curved outwards at the margin, with narrow foliar gaps; partly upon the massive dark brown bands of sclerenchyma surrounding these bundles; partly upon the large number of thin foliar bundles, or the presence of one or a few broad channel-shaped ones; finally upon the very oblique ascent of the foliar bundles through the cortex, and the frequent anastomoses in this part of their course between those belonging to one leaf (comp. Fig. 141, p. 293). If the internodes are short the transverse section shows a circle surrounding the pith, composed of bundles elongated in the direction of the periphery, or curved outwards in a horseshoe-like manner, and with brown sheaths: between these are medullary rays of unequal breadth, according as the section has passed through foliar gaps at varying height; outside the ring of bundles are those bundles which are passing to the leaves; where the internodes are elongated and the foliar gaps are of relatively small size, the transverse section may show one closed annular bundle, which is only broken here and

[1] Hofmeister, *l.c.*

[2] Mettenius, Angiopteris, p. 524.

there (by a foliar gap), and opposite these points are foliar bundles in the cortex, such as Karsten[1] illustrated in the case of Alsophila pruinata.

Sect. 83. If the structure just described for stems with leaves in several rows be imagined to be transferred to horizontally growing stems with leaves alternating in two rows, there are thus obtained foliar gaps in two alternating rows right and left,

Fig. 134.—Davallia dissecta; rhizome; slightly magnified. *A* vascular bundle-system, the cylindrical surface reduced to a single plane; *o* upper bundle, *u* lower bundle, *b* point of insertion of a leaf, at × point of origin of a lateral shoot; *B* transverse section. After Mettenius.

Fig. 135.—Aspidium coriaceum; rhizome; slightly magnified; after Mettenius. *A* bundle-system, the cylindrical surface reduced to a single plane; meaning of the letters as in Fig. 134. *B* transverse section.

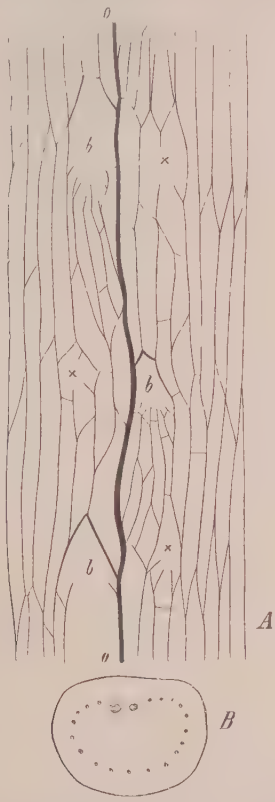

Fig. 136.—Polypodium fraxinifolium; rhizome; slightly magnified; after Mettenius. *A* bundle-system, the cylindrical surface reduced to a single plane; *o* upper bundle, *b* insertion of a leaf, × points of origin of the lateral shoots. *B* transverse section.

limited by one bundle with a median upper course, and by one median one below, and by alternating transverse bundles between the two. This arrangement is found in many forms as described, or with unimportant modifications[2]. Comp. Figs. 134, 135.

[1] Vegetationsorg. d. Palmen, Taf. IX. fig. 1.

[2] Mettenius, Angiopteris, p. 544. Special deviations and irregularities described by Trécul, *l. c.*

Their creeping rhizome shows a circle of bundles in transverse section. Of these, one passing along the middle of the upper side (the *upper bundle*, *o* Figs. 134, 135) and a second passing similarly along the under side (the *lower bundle*, *u*) are distinguished by their band-like form and greater size from the other weak ones, which are opposite to the two rows of leaves. Both the stronger bundles are connected regularly, at distances corresponding to those separating the leaves, by transverse bundles curved convexly upwards, or bent at an angle, so as to form a net, the meshes of which are the foliar gaps. From the margins of these arise (in addition to the bundles for the lateral shoots *x*) the foliar bundles (*b*) which converge opposite the point of insertion of the leaf, which is usually relatively small, and run almost radially perpendicular in the stem up to that point: these bundles may anastomose one with another, and with the upper and lower bundles by solitary thin transverse connections. The transverse sections of the foliar bundles are the small bundles seen in the transverse section of the stem; they there form together with the upper and lower bundles either a circle, as above stated, or in flattened stems an elliptical figure, which is often compressed in such a way that the upper and lower bundles have a central position, while the foliar bundles are outside.

The arrangement described occurs in a simple form, with specific modifications as regards the number of the foliar bundles, the form of the gaps, strength of the bundles, &c., in Asplenium obtusifolium, A. resectum, Acrostichum brevipes, A. Lingua, A. simplex, A. Melanopus, Polypodium altescandens, P. tenellum, Nephrolepis ramosa, Aspidium albopunctatum, A. coriaceum (Fig. 135). In the Davallias there arises the further complication, that the branches springing from the margin of the foliar gap do not run directly or with unimportant anastomoses to the leaf, but first form a network of fine bundles, which stretches over the foliar gap, and sends a certain number of branches into the leaf. According to the number of these foliar bundles (which varies according to the species) the network is simpler (D. parvula, pedata, heterophylla), or more complicated, and with more numerous meshes (D. bullata, dissecta (Fig. 134), elegans, pyxidata, canariensis, &c.).

A more considerable deviation from the structure described appears in other creeping stems of Ferns with leaves in two rows: here, not only is the foliar gap covered in by a network of bundles, but also instead of the lower bundle two or more reticulately anastomosing bundles are present, and the lower bundle is as it were split up into a network of bundles (Fig. 136). Where the number and arrangement of the bundles are very simple, as e. g. in Polypodium aurisetum, piloselloides, cayennense, or where the upper and lower bundles and their transverse connections bordering on the foliar gaps are strongly distinguished from the rest by their size, as in Platycerium alcicorne, the structure may be referred easily to the scheme with upper and lower bundles. But often the upper and lower bundles and all the anastomoses are of such uniform strength, and the meshes of different order so irregular, that the foliar gaps can only be distinguished at both sides of the upper bundle, where the bundles pass out into the leaves. In place of the tube regularly perforated by foliar gaps there is in extreme cases as it were a complex irregular network, the relations of which to the more simple type can only be recognised as indicated by the regularly alternating 'foliar meshes' *b*. As extreme examples may be named, Polypodium vulgare, sporadocarpum, aureum; numerous species of

Polypodium and Acrostichum axillare show numerous intermediate forms between these and the simple scheme with upper and lower bundles. For further details cf. Mettenius, Angiopteris, p. 552, &c., Taf. VII–X.

b. Several concentric rings of bundles.

Sect. 84. A number of Fern-stems with leaves in many rows—species of Pteris, and Saccoloma, Marattiaceæ, Ceratopteris—show in the transverse section of the stem several concentric rings of bundles, similar to one another in form and thickness. As far as is known, these cases are connected with those forms above described, in which the bundles running from the ring to a leaf pass gradually, and for a long distance obliquely upwards through the cortex, and are connected by anastomoses both one with another, and also with those belonging to neighbouring leaves. The middle of the stem is traversed by one axile bundle, or in most cases by a relatively narrow tube of bundles, surrounding a narrow pith.

From these inmost bundles there arise at regular distances, and in close relation to the arrangement of the leaves, flattened or narrow bundles, which branch out at once into broad reticulate layers: these do not pass out directly into a leaf close to their point of origin, but run upwards and towards the surface of the stem through a number of internodes, and finally pass out into leaves, or divide into branches, which pass out in succession. Each of these layers of bundles has the form of a portion of the surface of a cone, which widens upwards: each is surrounded by a layer of similar form (and a zone of parenchymatous cortex separating it from the latter), and arises at its lower end from the inmost bundles. At the points of insertion of the leaves there are anastomoses between the successive zones, i. e. between those which are passing out, and the next inner ones, which run further. The rings which appear in the transverse section are the transverse sections of the conical zones: their number in any given transverse section depends upon their special course, particularly upon the inclination of the conical surfaces, which is closely connected with the elongation of the internodes.

The simplest case occurs in Pteris elata var. Karsteniana, and P. podophylla Sw.[1]; also in P. Orizabæ, and P. gigantea[2]. In the two first-named species there is, according to Mettenius, a second narrow bundle-tube within an outer one, the former being split sometimes on one, sometimes on two sides. Portions of the latter curve directly outwards into the leaves; portions of the first, turning outwards, enter the gaps formed by the passing out of a portion of the outer ring, and coalesce with the outer tube, which rises laterally from the base of the leaf.

In Saccoloma inæquale there is a similar arrangement (Mettenius). Saccoloma adiantoides[3] shows in transverse section (Fig. 137) at least three closed or split rings representing so many conical zones, of which the outermost alone gives off broad and flattened concave portions into the leaves (closely arranged with $\frac{2}{5}$ divergence); the middle one, curving outwards, enters the gaps thus formed; finally the inner one fills up in the same way the gaps made in the middle one by this outward curvature.

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[1] Mettenius, Angiopteris, p. 535, Taf. VI. 12–16.
[2] Karsten, Vegetationsorg. d. Palmen, *l.c.* p. 193.
[3] Mettenius, *l.c.* p. 531, Taf. VI.—Karsten, *l.c.* p. 194 (Dicksonia Lindeni).

The inmost of these zones differs in individual cases: in some, investigated by Mettenius, it is composed of two flat small bundles, which appear curved in transverse section; in others, on which Karsten's statements appear to be based, there is a solid cylindrical bundle. Karsten says of this that it ends freely in the pith below: this does not coincide with the data given above, chiefly after Mettenius, and requires further examination.

Of the Marattiaceæ with several rings of bundles as seen in transverse section, the cylindrical stem of the species of Danæa with on an average three rings in transverse section, may according to the notes of Mettenius[1] belong to this category. Of the three rings the outer consists of numerous filamentous bundles, the two others of broad and flat ones. These stems however require more exact investigation. The same may be said of the inverted conical-shaped thick tuberous stem of Angiopteris evecta[2], of which Mettenius has thoroughly investigated and described one large specimen only. Transverse sections of the stem show 5–6 irregular zones or rings which pass over one into another. From an irregular network of bundles surrounding the pith bundles arise in a succession corresponding to the arrangement of the leaves, and pass obliquely upwards and outwards; each of these soon becomes wider, and splits into a rather irregular network rising obliquely outwards and upwards, and having the form of a portion of a conical surface, the bundles of which are reticulately connected with those of neighbouring equivalent portions. A number of branches, derived from that zone which is at the time the outermost, enter the base of each leaf (into the back and sides of its basal part), and, to take the place of those which have passed out, a corresponding portion of the next inner zone passes upwards into the outward zone from below the axils of the leaf in question, and of the two next lower lateral leaves. Portions of the third zone enter the gaps thus formed in the second, and are reticulately connected with the next outer zone. Further anastomoses between the branches of the successive zones are formed at the very point of insertion of the leaf, and two bundles belonging to the inner side of the base of the leaf are given off from the second zone, which enters the gaps of the outer zone. In the stems investigated the lower zones had small, almost cylindrical bundles, which formed wide-meshed irregular nets; the upper zones (near to the stationary end of the dead stem) had broad flattened bundles with narrow reticular meshes; the zones of intermediate position were also intermediate as regards the reticular form; the bundles which enter the leaves were of similar form to those of the zones from which they arose. Accordingly transverse sections showed at different heights either several concentric annular zones, often irregularly connected by oblique bands (the portions cut through in their course into outer zones), consisting of small roundish bundles separated by abundant parenchyma—corresponding to the usual arrangement in the tuberous stems of Marattiaceæ; or on the other hand rings, of which the outer at least consist of broad flattened pieces, separated by some few bands of parenchyma. For further peculiarities, comp. Mettenius, *l.c.*

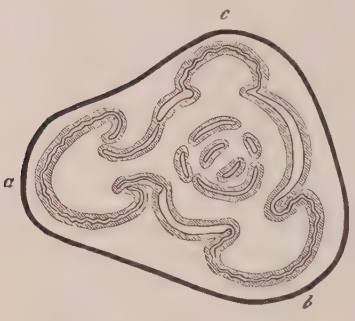

FIG. 137.—Saccoloma adiantoides; transverse section through the stem; after Mettenius; natural size. At *a* the band-like vascular bundle of a leaf, just separated from the outer ring; *b* and *c* bundles of two successively higher leaves, appearing as protrusions of the outermost ring. The bundles which enter the leaves are finely undulated. The bundles of all rings are surrounded by a sheath of darker, thicker walled parenchyma In my specimens the inmost ring of bundles is sometimes narrow, sometimes it is replaced by a single round bundle.

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[1] *l.c.* p. 524.—Compare also Brongniart, Archives du Muséum d'Hist. Nat. tom. I. p. 439, Tab. XXXIII, and Karsten, Vegetationsorg. d. Palmen, Taf. IX. fig. 10.

[2] Brongniart, *l.c.*

The investigation of a *young* stem of Angiopteris showed me a completely typical bundle-tube, interrupted by wide foliar gaps; two strong foliar bundles arise below at the lateral margins of the gap, and ascend obliquely through the cortex, within which they divide into the branches which pass out into the leaf.

The concentric zones of thin bundles in the stem of Ceratopteris thalictroides may also belong to this category, but require further investigation. Comp. Mettenius, *l. c.* p. 530.

c. Accessory medullary and cortical bundles in addition to the simple tube of bundles.

Sect. 85. Among the *Cyatheaceæ*, according to Mettenius, the above-mentioned forms (p. 286) have only the typical tube, perforated by foliar gaps, and consisting of flattened vascular bundles, the margins of which next the gaps are curved outwards. Other species, including the majority in the genera Cyathea and Alsophila, have, in addition to the vascular bundles thus disposed, small bundles, which originate from the foliar gaps and traverse pith and cortex, there forming a delicate open network. The relatively thin bundles from the margin of the foliar gap, which pass into the petiole, arrange themselves so that in a transverse section of its insertion, or in the leaf-scar, they are arranged in a curve, convex downwards, and simple, or with the ends turned inwards above: it consists of few bundles in small leaves, e. g. in young specimens of Hemitelia capensis 13–14 bundles, of Alsophila radens Klf. 4, Cyathea arborea Sm. 13[1]; on the other hand, in strong specimens or species they form two curves with the ends curved inwards, and consisting of many bundles, one of these curves being convex downwards, corresponding to the lower edge of the foliar gap and springing from it, the other convex upwards, and corresponding to the upper margin. The incurved ends of both curves are directed downwards and towards the middle of the leaf-scar so that their bundles form on each side two nearly parallel series running to the middle of the scar[2]. Compare Fig. 138.

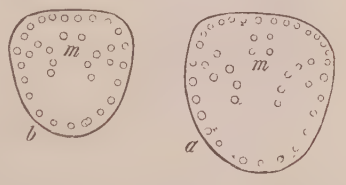

Fig. 138.—Cyathea Imrayana; natural size. Two old leaf-scars from a dead stem; *a* lower, *b* higher on the stem; *a* with four, *b* with two medullary bundles above *m*.

Further, in the space surrounded by the single curve or by the upper one, a relatively small number of bundles pass out into the petiole—e. g. as described by Mettenius in Hemitelia capensis, Alsophila radens, and Cyathea arborea two each, in a species of Cyathea 7, in Alsophila Haenkei 4, in Cyathea Imrayana 2 or 4, in C. ebenina 2. These do not arise from the margin of the foliar gap, but are connected both inside and outside it with the margin itself, as well as one with another, by numerous strong anastomoses (usually sheathed with sclerenchyma): they then run through the foliar gap downwards into the pith. (Figs. 139, 140, *m*.)

Immediately after their entry they pass with a steep curve inwards and downwards, and divide into branches diverging acutely downwards; these sometimes

[1] Mettenius, Angiopteris, *l. c.* Taf. V.

[2] Mohl, in Martius, Icones, *l. c.*, Verm. Schriften, p. 110.—Numerous valuable details in Trécul, *l. c.* XII. p. 270.

pass on further in the middle, sometimes at the periphery of the pith, and some insert themselves at an acute angle on similar branches from lower leaves, others end blind. At the foliar gap the bundles, which are themselves about as thick as a bristle, are surrounded by brown sclerenchyma, or supported by it on one side, and these sheaths of sclerenchyma, which are closed or open on one side, accompany the bundles for a long distance downwards; sometimes they also anastomose with

FIG. 139.—Cyathea Imrayana; natural size. From a dead stem, the soft parts of which had rotted away; the stem is halved longitudinally, and seen from within. The figure shows a piece of the tube of vascular bundles with one foliar gap, *l—l*, and a leaf-scar exactly halved longitudinally. From this the bundles of sclerenchyma which accompany the vascular bundles may be seen to branch off, and from there those which accompany the medullary bundles arise as branches and pass down into the pith with many branchings and anastomoses; some of them have blind pointed endings; the one which extends furthest downwards has anastomosed with one coming from a lower leaf. Of the bundles which end at the leaf-scar, *m* originates from the pith, the rest from the margin of the foliar gap.

FIG. 140.—Cyathea Imrayana; axile longitudinal section through the same stem as Figs. 141 and 142; natural size. The section is about 3 mm. thick, and for the most part transparent; the *black* bands of sclerenchyma and *pale* vascular bundles here represented in one plane do not all lie exactly in this plane, but are all near it. Certain parts of the chief sclerenchymatous-sheath *s—s'* which show through, and at the bottom two portions of the surface of the stem seen obliquely, are shaded off as they pass from the surface of section. The letters *a*, *s*, *s'*, *f* have the same meaning as in Fig. 141; *r* cortical bundles, *b* leaf-scars, *bl* vascular bundles passing out into leaves, *w* insertions of roots, *m* a foliar bundle running into the pith; above × blind ending of a medullary bundle (examined under the microscope).

similar sheaths, which descend from leaves side by side with or below them, sometimes they diminish downwards and end blindly in a point, while the vascular bundles continue their downward course alone beyond these endings (comp. Fig. 140).

According as they follow the first or the second course, the sclerenchymatous sheaths themselves form either a tough net traversing the whole pith, as e. g. in the case of a stem which is before me under the name of Cyathea ebenina, or they pass from each leaf inwards and downwards as a sheaf of bundles, with blind and pointed ends, which show frequent anastomoses one with another, but only fewer or quite solitary anastomoses with the sheaves of bundles belonging to other leaves: e. g. Cyathea arborea, Hemitelia capensis (Mettenius), C. Imrayana, and most other species; in Alsophila microphylla and villosa the vascular bundles in the pith are only accompanied by isolated spindle-shaped bundles of sclerenchyma, which are not connected into sheaths till the foliar gap is reached (Mettenius). In most of the dried stems, when subjected to investigation, the delicate unsheathed parts of the vascular bundles cannot usually be seen, the tough sclerenchymatous bands alone being clearly preserved. Since, as above stated, the course of these bands is a copy of that of the vascular bundles, the description given for the latter will suffice also for them.

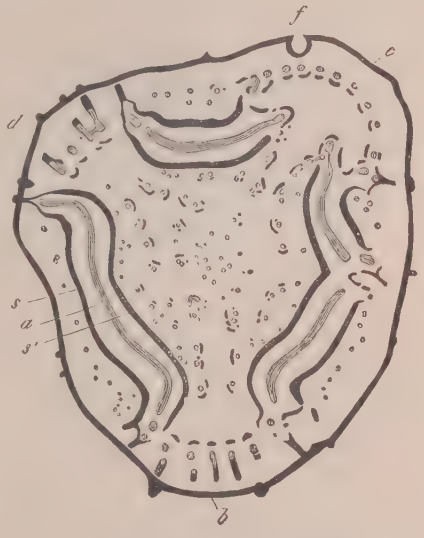

FIG. 141.—Cyathea Imrayana: transverse section through the living stem; natural size; seen from above. At *b*, *c*, *d*, foliar gaps. All *quite black* bands and points are transverse sections of sclerenchyma; all the paler ones are vascular bundles. In and near the foliar gaps, especially *a* and *b*, are root-bundles going to the periphery; *f* channels at the base of the leaf; *a* vascular bundles of the main tube; *s* outer, *s'* inner plates of its sclerenchymatous sheath. Inwards from *s'* the pith with its bundles; outwards from *s* the cortex with its bundles.

Many but not all species have, besides the medullary bundles, accessory cortical bundles also. In C. Imrayana (Fig. 142) these arise from bundles which pass into the leaves, and close above their point of departure from the foliar gap, and in fact from most, but not from all those which branch off from the lateral and lower margin of the gap. They descend with a steep curve from their point of origin into the parenchyma of the cortex; some of them, after pursuing an individual course for a short distance, unite each with another coming from the same foliar gap; most of them however pass almost straight downwards in the middle of the cortex, and in the neighbourhood of the adjoining lower foliar gaps they either affix themselves at an acute angle on bundles which there arise, or they end blindly. The cortex is accordingly traversed by a network of bundles with elongated meshes, which are sometimes quite closed, sometimes open on one side. In the stems in question the cortical bundles, of the thickness of a bristle, usually have no sclerenchymatous sheath; some few, especially those which arise from the upper part of the lateral margin of the gap, are however often accompanied for about 1^{cm} from their point of origin by such a sheath, in the form of a channel, which is open outwards; comp. Fig. 142. In a dry strong stem, bearing the name C. Imrayana (not the same used for the accompanying figures), a structure similar to that just described can still be clearly seen.

But in this case there is this further peculiarity, that from the upper part of each lateral margin of a foliar gap two or several bundles arise, which unite after a short course into one, and that these bundles from their point of origin onwards are surrounded by a thick sheath of sclerenchyma. Together with the latter they form on each side of the foliar gap a cone several millimetres thick at the point of origin; they either taper to a point towards the adjoining lower gaps, and end blindly in the parenchyma, or coalesce with the margin of the adjoining lower gaps, and with a cone which there arises. The sclerenchymatous sheath of the cone shows slits here and there, through which unsheathed branch bundles emerge and turn downwards. Cones, fundamentally similar to those described, the points of which end blindly in the cortex, and indicate with certainty the presence of a system of cortical bundles similar to that in C. Imrayana, were first found by Mettenius[1] in a dry stem of Alsophila Haenkei. In other species a system of cortical bundles is unknown, partly because of the difficulty of finding it in dry stems subjected to investigation; in many species however (for instance Cyathea arborea and Alsophila microphylla may be named with certainty) it is altogether absent.

FIG. 142.—Cyathea Imrayana; piece of a living stem with four bases of petioles, the outer layers of cortex being peeled off; seen from without. The margins of four foliar gaps, the bundles which arise from them and pass into the leaves, with the young roots (black) seated upon them, and the bundles which descend through the cortex, are exposed; the latter and the roots are quite free, the rest covered by a little transparent parenchyma, through which they are clearly seen, and all the parts are held together in their natural position. Natural size.

SECT. 86. Most species of *Dennstædtia* have, as above indicated, a simple tube of bundles which is closed with the exception of the narrow foliar gaps. Within this, and near the upper side in the horizontal stem, there are in the pith of D. rubiginosa one, in D. cornuta several small bundles with circular transverse section, in D. cornuta these form a tube alternately closed and again split into 2–3 bundles. At the base of a shoot the medullary bundles arise from the inner surface of the tube, at the foliar gap they approach the latter, and divide into a few branches, of which some anastomose with the margin of the gap, others enter the leaf with those which start from the gap, the third series (or single bundle) ascending further in the shoot as medullary bundles[2].

The somewhat more complicated arrangement in Chrysodium vulgare, on which compare Mettenius, *l. c.*, may be placed in connection with the above.

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[1] Angiopteris p. 528, Taf. V. A good figure of a transverse section of a Fern stem with cortical bundles is given by C. H. Schultz, Mém. présent. de l'Acad. des Sciences, tom. VII (1841), pl. 22.

[2] Mettenius, Angiopteris, p. 540.

Sect. 87. While in the last-named cases accessory medullary bundles occur, and in many Cyatheaceæ accessory medullary and cortical bundles in addition to a typical tube of bundles, there is found in *Pteris aquilina* and *Polybotrya Meyeriana* a bundle-tube constructed as in the type with a strong upper bundle, and this is strengthened by a much divided cortical system of bundles.

In the seedling of Pteris aquilina[1], till the development of the seventh or ninth leaf, there is one axile bundle, which traverses the stem starting from the point of union of the first leaf with the first root: in transverse section it is deeply grooved, and half-moon-shaped: bundles pass from it into the leaves; after the formation of the seventh to ninth leaf 'the stem forks.' Both branches of the fork increase rapidly and considerably in thickness, and the course of the vascular bundles in them is altered. The lateral opening of the axile bundle is widened, then the upper half is separated from the lower; there are now two bundles, an upper and a lower one, which split now and again into thinner branches, while these are soon again united. When the branches of the fork have attained the length of about 6cm, and a thickness of about 4mm, weaker branches come off from both the bundles: these run near the surface (in the cortex), and here form a peripheral network with long and narrow meshes, in which the upper central bundle is distinguished from the rest by its greater width. This structure is retained by the mature rhizome (Fig. 143): the number of the peripheral bundles rises to twelve in the transverse section. Two thick brown plates of sclerenchymatous fibres lie between the inner and outer systems of bundles, and are only separated from one another at the two sides of the stem by a narrow slit filled with parenchyma: they are often joined at one side, often even all round so as to form a closed tube. Branch-bundles from both nets of bundles pass into the leaves and branches: roots arise from the outer ones only. At those points of exit, as also at the base of the petiole, the two nets anastomose by single transverse bundles. Throughout the whole of the rest of their course they are without connection with one another in many weak specimens; in strong rhizomes, according to Stenzel, thin connecting bundles pass from the margins of the inner bundles to the lateral outer bundles, while the upper and lower bundles of both systems are connected by single short branches, which pass through holes in the bands of sclerenchyma.

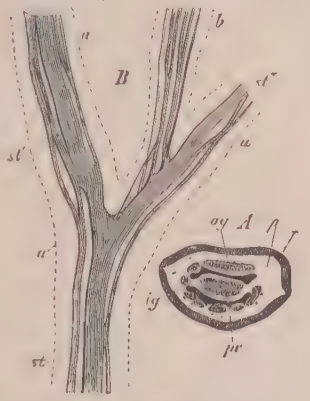

FIG. 143.—Pteris aquilina; stem (rhizome); slightly enlarged. *A* transverse section, *r* brown sclerenchymatous layer of outer cortex, *p* colourless soft parenchyma, *ig* vascular bundles of the inner zone, *ay* the broad upper bundle of the outer zone, *pr* the plates of brown sclerenchyma separating the two zones. *B* the upper main bundle of the outer zone of the stem (*st*) and its branches (*st'*, *st''*), with the branch bundles which pass into a leaf (*b*) prepared free; *u*—*u* outline of the stem.

In the main axis of Polybotrya Meyeriana[2] an inner network is found surrounding a narrow pith, and composed of 3–7 strong bundles arranged in a circle when seen in transverse section; it corresponds in composition to that above

[1] Hofmeister, *l. c.* p. 620.—Mettenius, Angiopteris, p. 561.—Stenzel, *l. c.*
[2] Mettenius, *l. c.* p. 559, Taf. VII.

described for the Polypodiaceæ with a reticulately divided lower bundle, having long narrow, rather irregular meshes: foliar meshes and points of origin of lateral shoots appear only in regular alternation, on both sides of a clearly distinguishable upper bundle. Outside this net is a peripheral one, showing in transverse section fifteen to about fifty bundles, which rarely form a single circle, but are usually arranged at the upper side of the stem in 2–3 irregular series, at the lower side of the stem in a curve. The bundles of the peripheral net are thin and connected in elongated meshes, in the arrangement of which there was as little regularity to be recognised as in that of the obliquely ascending connecting-bundles, by which the outer net is joined with the inner at many points. Three branches arising from a single mesh of the inner net and 9–12 peripheral ones enter each lateral shoot; into the base of the leaf there pass two or several inner, and 9–24 outer ones. All roots arise from the outer net.

c. *Bundle system in the leaves and foliar expansions.*

Sect. 88. The bundles, which leave the bundle-cylinder of the stem and pass out into the leaves, run as a rule towards the margin and apex of the leaf.

The bundles may run from their point of departure from the cylinder of the stem onwards, just as they did in the latter, as for instance in a leaf of a Conifer, where one bundle passes out from the cylinder and runs without division up to the apex of the leaf; or divisions of the bundles and coalescences of separate ones may occur at any point, so that the number to be seen in the transverse section of the leaf is not the same as at the point of exit itself. Examples of this, when it takes place in the node itself, have been given above, Sect. 61; in the case of their further course the phenomenon is universally known, and will be treated in detail in the following paragraphs.

In most cases the bundles at the *nodes* pass, without division, or after splitting into branches which run side by side, through the cortex into the leaf. But in certain individual cases there appear special branches at the node itself, which lie in the parenchyma of the cortex; these are here connected into a net or a transverse girdle; often branch bundles pass downwards from the node into the cortex of the adjoining internode.

Branches *peculiar to the node* (which do not pass out from it) are often found where several bundles emerge, forming oblique or curved connections between these. This is the case both in many traces with numerous bundles, belonging to solitary (alternating) leaves, e. g. Lathyrus Aphaca (comp. p. 240), where the median bundle has a curved transverse connection with the lateral ones; Viola elatior, Platanus, which will be mentioned below: also in whorls of two or more with leaves having one or more bundles. In the case of leaves with one bundle Hanstein[1] found a transverse girdle connecting the bundles at the node in numerous Rubiaceæ with whorls of two or more members (species of Asperula, Rubia, Galium, Hamelia chrysantha, Houstonia coccinea, Bouvardia mollis); on the other hand, other Rubiaceæ (Coprosma ligustrina, Exostemma floribundum according to Hanstein) show no transverse girdle. In whorled leaves with several bundles transverse girdles have

[1] Ueber gürtelförmige Gefässstrangverbindungen, Abhandl. d. Berliner Academie, 1857, p. 77.

been above described (pp. 257–259) in Calycanthus and Melastomaceæ. Hanstein found them in Sambucus, in species of Valeriana, Centranthus, Valerianella; Scabiosa, Knautia, Succisa, Dipsacus; Dahlia, Bidens cernua, and tripartita; Guizotia oleifera; and Nägeli in Humulus. In most plants with opposite leaves, e. g. the Labiatæ, Asclepiadeæ, Caryophyllaceæ, Caprifoliaceæ excepting Sambucus, many Compositæ and others enumerated by Hanstein, the transverse girdles do not occur.

Branch bundles *passing down through the cortex* may here be mentioned, and have already been described above for many Cyatheaceæ. Also in the strict sense the medullary bundles of these latter Ferns belong to this category, as being 'appendices' which run downwards from the bases of the leaves. Among the Monocotyledons no examples belonging strictly to this series are known, still the bundles running through the cortex, as described above for Bromeliaceæ and Palms, correspond in their course to some extent to those under discussion. The same may be said of the above-described cortical bundles of Melastomaceæ and Calycanthus. Among the Dicotyledons, however, branches passing downwards from the node through the cortex occur elsewhere; in the first place in the foliaceous corners of the so-called winged stems, e. g. in species of Lathyrus (L. silvestris, latifolius, Nissolia, &c.), secondly, and in the most striking manner, in many (but by no means all) succulent plants: Salicornia, species of Mesembryanthemum, Cacteæ. The course and ramification of the bundles in these cases and in the winged corners closely resemble that to be described in the leafy expansions, the cortex here assumes completely the anatomical (and physiological) properties of foliar expansions.

In the species of Salicornia[1] the short scaly leaves are arranged in decussate pairs. One bundle, which splits up immediately at its point of exit into three branches, passes from the node into each leaf: of these a single median one runs to the apex of the leaf-scale, and a lateral one on either side passes perpendicularly downwards into the cortex. These branches, of which there are six for each pair of leaves, give off throughout their whole course numerous ramifications, which anastomose frequently in a reticulate manner. From the apices of the leaves downwards the cortex of the whole internode, which attains a length of 2^{cm}, is traversed by a tubular network of bundles, which is closed (not interrupted as stated by Duval), and which ceases immediately above the next lower node, without any connection with that which there arises. In many species of Mesembryanthemum, e. g. M. imbricatum, M. crystallinum, &c., but by no means in all species of the genus, thin branch bundles, divided into reticulately anastomosing branches, pass downwards from the node into the cortex; here again they do not reach the next lower node. In Cacteæ, Epiphyllum truncatum, species of Cereus, Mamillaria, the above-mentioned (p. 261) Rhipsalidaceæ[2], &c., reticulately connected branches come off from the main bundles, which run to the apex of the rudimentary leaves, and pass through the cortex, forming a continuously anastomosing network between the neighbouring main bundles.

The bundles, which enter *stipules*, and other *appendages of the base of the leaf* which often have a glandular surface, usually arise as branches from those which enter the main leaf (e. g. Prunus, Passiflora, Tropæolum, Medicago, Liriodendron[3],

[1] Duval-Jouve, *l. c.* (see above, p. 226).

[2] Vöchting, *l. c.*

[3] Nägeli, Beitr. *l. c.*

Coprosma ligustrina, Exostemma floribundum[1], Quercus[2]); from the anastomoses at the node; or from the transverse curves, e. g. in those Rubiaceæ which have them, as is seen in an especially striking way in the large leafy stipules of the Stellatæ, and in Sambucus Ebulus (Fig. 44), &c.

In less common cases special lateral bundles of the composite leaf-trace, which traverses the stem, pass into the stipules[3]. In Viola elatior one lateral bundle of the three forming the leaf-trace passes into each stipule, and in addition branches from curved transverse anastomoses, which appear in the node between the bundles of one trace. In Platanus occidentalis the sheathing stipule has 7–9 bundles at its base; of these the two stronger lateral ones arise from the outermost lateral bundles of the leaf-trace (which has 7–9 bundles), the rest unite to two, sometimes to one or three bundles, which separately enter the bundle-ring of the stem. In Humulus Lupulus[3], of the three bundles of each leaf-trace which enter the stem, the median one passes into the petiole, and each lateral one into a stipule as its middle nerve. Each lateral one is connected at the node by a transverse bundle on the one hand with its median bundle, on the other with the lateral one of another (opposite) leaf; from the transverse girdle thus formed the lateral nerves of the stipules are given off in regular succession, so that the girdle itself is compounded in a sympodial manner of outwardly curving bundles.

FIG. 144.—Sambucus Ebulus, after Hanstein. Scheme of the bundle system in two successive internodes: the cylindrical surface reduced to a single plane. Leaves in decussate pairs; each leaf receives one median bundle, *h*, and on either side two lateral ones, *s'*, *s''*; of these the inner stronger one, *s'*, descends undivided into the internode; the outer one, *s''*, divides in the node into two shanks; one inner one which pursues a solitary course downwards, and an outer which coalesces at once with the similar one of the opposite leaf (*z*). By this union in the node the transverse girdle is formed, from which the bundles *n* pass into the stipules. The further course of the leaf-trace of each pair, which consists of twelve bundles, is obvious on study of the figure. From Sachs' Textbook.

SECT. 89. The bundles run as a rule straight through the *petiole* towards the lamina. When they are numerous they are here also branched and connected by anastomoses. The bundles, when more than one, are arranged on the transverse section either in a curve open upwards, or in a ring, or distributed over the whole surface of transverse section. Large leaves, e. g. of Leguminosæ, Umbelliferæ, Palmæ, Aroideæ, Cycadeæ, Ferns, &c., yield various special examples of these relations, which have been often made use of in the Ferns for systematic purposes[4].

SECT. 90. In the lamina of leaves, whatever their form, in the peripheral leaf-members of any stem, and in the leaf-like branches (Phyllodes, Phyllocladia, &c.),

[1] Hanstein, *l. c.*

[2] A. B. Frank, Botan. Zeitg. 1864, p. 378.

[3] Nägeli, *l. c.* pp. 75, 92, 114.

[4] Compare e. g. Grew, Anatomy, Tab. 49.—Presl, Gefässbündelvertheilung im Stipes der Farne, Abhandl. d. k. Böhm. Ges. d. Wissensch. 5. Folge, Bd. V.—Reichardt, in Denkschr. d. Wiener Academie, Bd. XVII. - Duval-Jouve, Et. sur le pétiole des Fougères, Hagenau, 1856.—Trécul, Ann. Sci. Nat. 5 sér. X and XII, and the descriptive literature of Ferns.—Reichardt, Ueber d. centr. Gefässbündelsystem einiger Umbelliferen, Wiener Acad. Sitzungsberichte, 1856.—A. B. Frank, Botan. Zeitg. 1864, p. 380. [De Candolle, Anatomie comparée des Feuilles, Geneva, 1879.]

parts which will all be included under the term *leaf-expansions*, the bundles distribute themselves along the surface, sometimes ending free, sometimes anastomosing with one another in a reticulate manner.

The bundles, especially those in the flattened expansions, lie as a rule in the protrusions or ridges of the surface, which are known as *nerves*, *ribs*, or veins. The course of these, the *nervation* or *ribbing*, and that of the vascular bundles often exactly coincide, both phenomena are therefore usually indicated by the same name. There is no further objection to this convenient use of the term; but it must be pointed out that two different phenomena are thus dealt with, one belonging to the external formation of the parts, and referring to the relief of the surface, and another, which refers to the inner structure; and that though the two phenomena are always closely correlated, they do not coincide always, or in all points.

The phenomena of surface-relief as seen in coarse ribbing may be here assumed as known, the reader being referred to the literature on this subject, especially to that of Pteridography and Palæontology[1]. In treating of the arrangement of the vascular bundles we must take into consideration (1) the divarication of the bundles, that is their course in the direction of the surfaces of the leaf-expansions (Sect. 91); (2) their position—as seen in a transverse section—within the other tissues (Sect. 92).

Sect. 91. As regards the divarication of the bundles it must be premised that for the middle portion (Rachis, Petiolus communis) of compound and deeply-divided leaves, and for the main ribs of many, especially of large leaves, the same rules hold good as have been above stated for the course of the bundles in the petiole. The bundles are continued from a petiole, which contains several bundles, into the main nerve, and here are arranged in a channel open upwards, or in one or several circles, and are connected by anastomoses one with another: in their course towards the periphery some of them pass out into the branches of the nerves, others give off branches into them, while they decrease in number and size proportionately. The stronger lateral nerves of a lamina may also contain several bundles, e. g. Quercus pedunculata. A. B. Frank (*l. c.*) has given an exact description of the course of the bundles of the leaf in this plant, and notes on the same in other plants.

The bundles which pass into the foliar expansion, either as branches from the above-named parts, or directly from the nodes, either remain unbranched, or give off branches, often up to high orders, their strength diminishing as a rule with each higher order, but in a degree which varies greatly in each individual case.

The bundles and branches of whatever order either end free in the foliar expansion, or unite and anastomose with others.

Free ends sometimes lie at the *periphery* of the foliar expansion, in flat leaves especially at the margin and point, occasionally also at the surfaces: sometimes they

[1] As chief works and sources of information the following may here be cited: L. von Buch, Ueber die Blattnerven, and Die Gesetze ihrer Vertheilung, Monatsbr. d. Berliner Academie, 1852, p. 42.—C. von Ettingshausen, Die Blattskelete der Dicotyledonen, Wien, 1861, fol.; and the following articles of the same author from the Sitzungsberichten (S.) and Denkschriften (D.) der Wiener Academie: Apetalæ (D. XV); Papilionaceæ (S. XII); Bombaceæ (D. XIV); Celastrineæ (D. XIII); Euphorbiaceæ (S. XII); Loranthaceæ (D. XXXII); Gramineæ (S. LII. 1).—For the Ferns compare Mettenius, Filices Horti bot. Lipsiensis.

lie internally: *internal endings.* The bundles which end at the margin and point may be termed, in accordance with the terminology of the coarser nervation, apically directed (acrodrome) and marginally directed (craspedodrome). The points of ending of strong marginally directed bundles are often the ends of teeth and laciniæ. Anastomoses may appear between branches of any order, between equivalent and non-equivalent ones, and at any point of the foliar expansion. They give the bundle system the form of a net (reticulate veins), which varies greatly in individual instances. An allied special form, which is especially common in flat leaves, is found where anastomosing bundles describe curves close within the margin and following its outline: these are curved (camptodrome) bundles, according to the terminology of nervation.

The extremely various individual cases, which arise by various combinations of the above phenomena, group themselves under two main types, namely expansions with bundles having a separate course, which end free, without anastomoses; and such as have anastomosing bundles.

1. *Bundles with separate course and free ends* are found in the rudimentary and submerged leaves of many Angiosperms of the most various orders, in the foliar expansions of all Gymnosperms, with the exception of Gnetum and Stangeria, and in the leaves of many Ferns. One unbranched bundle, or the ramifications of branched ones, traverse the foliar expansion, and end free either internally or usually at the margin.

Rudimentary scale-leaves of Angiosperms often have their vascular bundles thus arranged, when they are present at all; the same may be said of the cotyledons of Monocotyledonous plants with one median bundle, or with two running near to the middle line, or with more than two. The cotyledons of Dicotyledonous plants have been but little investigated with regard to the relations in question, many have certainly a reticulum of bundles, even when they are 'single-nerved.' These most simple forms of leaves have been but little attended to in relation to the structural conditions under consideration. Of larger foliar expansions many submerged leaves of Dicotyledons (Batrachium, Myriophyllum[1]) with one bundle in each segment of a leaf belong to this series; also Pseudocallitriche with one median bundle[2]; Elatine Alsinastrum with one median bundle, which usually gives off some marginally directed branches into the narrow submerged leaves, &c.; similarly among Monocotyledons, e. g. the rudimentary simple median bundles of the Hydrilleæ. In the foliage of land-plants there is one simple apically directed bundle in each of the scale-like rudimentary leaves of the Casuarinas and of Arceuthobium, as also in those of Equisetum and Ephedra, which resemble them in habit.

Among Gymnosperms the foliar expansions of all Conifers[3] belong to this category: the leaves of the Cupressineæ, of Taxus, Phyllocladus, &c., with one median bundle; those of the Abietineæ which usually have two very close together, with median parallel course, rarely (Abies Pindrow) with one simple bundle; the double leaves of Sciadopitys with two which have a parallel course near the median

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[1] Askenasy, Botan. Zeitg. 1870, p. 196.—Vöchting, Myriophyllum, *l. c.*

[2] Hegelmaier, Monogr. d. Gattg. Callitriche, p. 31.

[3] Geyler, *l. c.* (see above, p. 245).—Thomas, in Pringsheim's Jahrb. IV. p. 43.—Strasburger, *l. c.*

line. The leaves of the broad-leaved Araucarias, and of species of Dammara and Nageia, have more than two bundles, which run unbranched from the base towards the apex, and end some of them at the apex, others below it. In Ginkgo the two bundles which pass from the petiole into the lamina, branch repeatedly into marginally directed forks. On Phyllocladus compare Strasburger, *l. c.*

The pinnæ of Cycas contain one median bundle, those of most Cycadeæ numerous unbranched bundles, which run parallel or slightly curved from the base to the apex. In Stangeria they are traversed by one middle nerve, in which 6–8 bundles run side by side; these give off branches laterally, which are arranged in a pinnate manner, and sometimes curve towards one another and anastomose close to the margin [1].

The leaves of Gnetum have, as far as is known, a typical reticulate bundle-system; in the leaf of Welwitschia there is a peculiar arrangement, which will be described below.

Among the Pteridophyta, besides the Equiseta already referred to, may here be cited the awl-shaped leaves of Pilularia, Isöetes, Lycopodium, and Selaginella; also the leaves and portions of leaves with fan-like, dichotomous, branched bundles, representing the Cyclopteris-nervation (e.g. Adiantum, Marsilia), and those with bundles branched once or repeatedly in a pinnate manner, all being disconnected and marginally or apically directed, which compose the nervation of Cænopteris, Ctenopteris, Pecopteris, Tæniopteris, Sphenopteris, Eupteris, and Neuropteris [2].

2. The foliar expansions with anastomosing bundles may be divided according to the arrangement of the latter into two subordinate types, which may be termed the *striated* and *reticulate*.

(*a*) In the striated type numerous bundles run separately and parallel along the leaf-expansion, the median ones running straight to the apex, the rest diverging the more from this straight course the nearer they are to the margin, and the more the boundary lines of the latter depart from parallelism. Most of these bundles curve towards one another close to the margin, and unite so that each one affixes its acroscopically-curved end on the basiscopic side of the one next it in the direction of the median line. Free ends are rare. Throughout their course the bundles are connected in a ladder-like manner by thin transverse branches. The former bundles may accordingly be called shortly longitudinal bundles, in contradistinction to the transverse branches. This arrangement is found, as far as is known, almost exclusively in the Monocotyledons and in the leaves of the majority of their families, also in the phylloclades of Ruscus and Myrsiphyllum, in the latter cases with transitions to the reticulate form. Some few families of Monocotyledons, such as the typical Aroideæ, Dioscoreæ, Taccaceæ, and many Smilaceæ, are exceptions. Of plants which are not Monocotyledons, the leaves of Welwitschia and of many narrow-leaved species of Eryngium, as E. pandanifolium, E. junceum, &c., belong to this category, or are at least allied.

According to the course of the longitudinal bundles we may here again distinguish two subsidiary forms, which are it is true connected by intermediate

[1] Kraus, in Pringsheim's Jahrb. IV. *l. c.*

[2] Compare Mettenius, Filices Horti Lipsiensis, p. 2, &c.

examples (e. g. in the Dracænas). In the one, which may be called the *longitudinally striated*, all the bundles run, in the manner indicated, separately from the base to the apex of the leaf or lamina. In the other, with *pinnate striation*, numerous bundles enter the midrib of a flat leaf, and pass through it towards the apex. They then pass one after another from the midrib into one or other half of the leaf, giving off numerous branches into it; only one or few of them extend to the apex of the leaf itself. All the bundles and branches which pass into the halves of the leaf are arranged in a pinnate manner, and have an acroscopically curved direction. The pinnate arrangement is characteristic of the group of Scitamineæ, of the broad-leaved Dracænas, Curculigo, many species of Hæmanthus (e. g. H. coccineus), Eucharis amazonica, &c. The longitudinally striated arrangement is characteristic of the majority of ordinary, linear, tapered leaves of Monocotyledons, also for the fan-shaped leaves of Palms, and the Foliola of the pinnate-leaves of the same family.

The longitudinal bundles which traverse the Monocotyledonous leaves of this category are often of almost equal strength, inasmuch as they enter the leaf from the stem as so many bundles of the trace, or from the node, as almost equivalent branches of one bundle of the trace (e. g. species of Potamogeton). On the other hand, it not unfrequently happens that they are not of uniform origin, some arising as branches from the others, but all pursuing fundamentally the same course. This has already been noticed above for the pinnately striated forms; the same occurs also in the longitudinally striated.

The longitudinal bundles of one leaf are not uncommonly of almost equal strength; in other cases of very unequal strength. In Palm leaves Mohl distinguishes bundles of three different strengths. Frequently one median bundle, which exceeds the rest in strength, is found in longitudinally striated leaves; in many leaves of Orchids with five and more projecting ribs (e. g. Stanhopea, Acropera, Maxillaria squalens) there is one bundle in each rib, which is distinguished by its size from the rest, which are not prominent. In the pinnately striated leaves of Heliconia farinosa, the ends of the bundles which pass out from the midrib are much stronger than their branches which pursue a similar course, a difference which cannot be recognised in similar leaves of allied plants, e. g. Phrynium setosum. From the example from the Orchidaceæ it cannot be concluded that in striated leaves generally the strength of projecting nerves must correspond to that of the enclosed bundles. In the keel-like projecting midrib of species of Carex, and in Pandanus pygmæus, there is a bundle, which far exceeds the rest in strength; in the thick midrib of Zea Mais and other large leaves of grasses there are several with the same arrangement as in the flat halves of the leaf, and resembling those which traverse the latter, with the exception of the rather stronger median bundle.

The transverse branches which connect the longitudinal bundles like the rungs of a ladder are often almost equal to them in strength,—e. g. Rhapis flabelliformis, Vanda furva,—but usually much weaker, being even reduced to a single vascular tube, or row of tracheides, for instance those in the pinnæ of species of Chamædorea, the leaves of Curculigo, Zea, &c., which are even hard to find. Their number on a given surface varies according to the species: on the average the distance between two may be about 1^{mm}, it is often greater, rarely they are much more closely arranged—in Phrynium setosum on the average 10–12 in a distance of 1^{mm}. They run either almost exactly transverse to the longitudinal bundles, so that the whole system of bundles consists of rectangular meshes; or they have a more or less oblique direction. Further, they pass either from one bundle to the next, or in very many cases they pass the next bundle, only touching it externally, and run to the second or third lateral bundle. It is often seen, especially in leaves with alternating stronger and weaker bundles, that they connect those of equal strength, running past the intervening ones of unequal strength. The transverse bundles

above described (p. 265) in the halms of many Monocotyledons have the same course as in the leaves.

It is only rarely that in leaves of Monocotyledons single transverse branches end blindly in the surrounding tissue. It is more commonly the case for a longitudinal bundle to arise as a branch from one of them.

The huge leaf of *Welwitschia* is traversed longitudinally by very numerous strong parallel bundles, these being connected in a ladder-like manner by transverse branches. The transverse branches either run at right angles from the longitudinal bundles, or obliquely, and sometimes directly and simply from one longitudinal bundle to the other, sometimes converging and anastomosing one with another in the narrow intervening spaces. Here and there a transverse branch ends freely in the parenchyma, without reaching the next longitudinal bundle; and from each of the transverse connections there often starts one short branch, which also ends blind in the parenchyma, and is always directed towards the base of the leaf (Fig. 145). The bundle-system is accordingly similar in most points to that of the longitudinally striated Monocotyledons, but the numerous internal free ends correspond to the usual condition in the reticulate Dicotyledons.—In the leaves of the above-named species of *Eryngium* only transverse branches between the parallel longitudinal bundles are found; in other similar narrow-leaved species, as E. aquaticum, there are also free endings and reticulate anastomoses.

FIG. 145.—Welwitschia mirabilis; piece of the network of vascular bundles in the leaf, prepared free; magnified about 4. *b* the edge of the piece nearest the base of the leaf.

(*b*) In the *reticulate* type (Fig. 146) the bundles which enter the leaf undergo branching of higher or lower order, and the branches are distributed over the whole surface, run in different directions, and are sometimes connected into polygonal or curved meshes, or sometimes end free, internally or peripherally. Meshes of higher order are enclosed in those of lower orders. The marginal sides of all marginal meshes form together in flat leaves a sympodial bundle, which follows the margin: this is more or less near to the actual margin, and is not uncommonly situated in the extreme margin itself (e.g. Quercus pedunculata, Banksia, Lauraceæ, Cocculus laurifolius, and many other coriaceous leaves). The bundles which end free internally arise as branches from the sides of the meshes, and terminate in the area enclosed by these, often after repeated short branching.

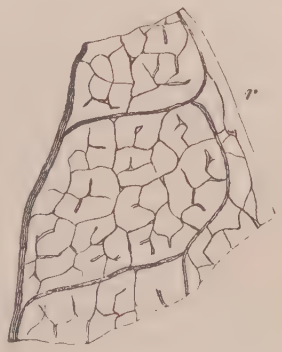

FIG. 146.—Psoralea bituminosa (40). The last branchings of the bundles in a piece of a leaflet; at *r* the margin of the latter.

As far as is known all foliar expansions of the Dicotyledons, with the few exceptions above quoted, belong to this type. The leaves of many land-plants, such as those of many species of Trifolium, which, from the appearance of their coarse nervation, seem to belong to the type with bundles pursuing a separate course, are still no exception; nor are the small linear "one-nerved" foliage-leaves of Dicotyledonous plants, such as species of Erica, Passerina, Fabiana imbricata. Among Monocotyledons the

Dioscoreæ belong to this type, and also many Smilaceæ, especially Smilax, Taccaceæ, Lapageria, Philesia, &c.; among the Gymnosperms, Gnetum; finally, the reticulate Fern-leaves, which represent in Pteridography the types of nervation of Goniophlebium, Phlebodium, Doodya, Marginaria, &c. The typical Aroideæ, the broad-leaved Potamogetons, and Hydrocharis belong also to this category, but appear as intermediate forms between the type under consideration and the striated type.

It is well known that the bundles of this type enter the expansion singly or several together in a midrib, which runs towards the apex, and give off from it branches of the first order, arranged in a pinnate manner, into the two halves of the leaf (Folia penninervia); or several separate main bundles diverge from the insertion of the leaf, and are also in their turn pinnately branched (Folia palmatinervia, peltinervia, triplinervia, &c.). The branches of higher orders are also sometimes arranged in a pinnate manner, sometimes they show (true or false?) dichotomy. The number of orders of branching usually ranges in the Phanerogams from five to eight. In the Ferns the branching is simpler in all respects than in the Phanerogams of this series.

It has already been noted above that branches of each order may end free or anastomose peripherally or internally. As regards the occurrence of these modes of ending the following cases occur:—

1. In rare instances reticulate connection between *all* branches, free ends occurring at most only in the apex of the leaf. In many succulent plants—species of Sempervivum, Mesembryanthemum—all free endings are absent, or at least have not hitherto been proved to exist: but an exact investigation of this point is still to be desired. But by no means all succulent plants belong to this type: Salicornia, e. g. has numerous internal endings in its cortical reticulum of bundles (p. 297), and the shrubby species of Crassula have numerous peripheral ones. Among Monocotyledons those Aroids which have been investigated (species of Anthurium, Pothos, and Monstera, Calla, Richardia) belong to this series, and further Hydrocharis and Potamogeton. All these have a free end at the apex of the leaf. In the two last-named genera the main bundles have a course similar to that of the longitudinal bundles of the striated type, the transverse branches which connect them are repeatedly branched, and the branches are connected into a net with angular meshes. In the Aroideæ also the course of the main bundles reminds us of that of the striated Monocotyledonous leaves. Between them branches of many orders form a complex angular network. Free internal ends are absent, or present only rarely here and there.

2. Free internal endings within the meshes, and no free peripheral endings. Close to the margin of the flat leaf runs the sympodial marginal bundle, which limits all the marginal meshes externally, and gives off no branches in a peripheral direction. The leaves of species of Ficus and Banksia, of Cocculus laurifolius, Buxus, Quercus pedunculata[1], and Psoralea (Fig. 146), may be named as examples of this phenomenon; apparently very many leaves, especially tough long-lived ones, with an entire margin, resemble these. Still I must cite no further examples, since the existing works on the coarser nervation do not permit of a certain decision whether short and thin free-ending bundles pass peripherally from the sympodial marginal bundle or not.

[1] Frank, Botan. Zeitg. 1864. p. 380.

3. Both internal and peripheral ends occur in all (?) Ferns of this category, though in many (e. g. Ophioglossum vulgatum, pedunculosum, Platycerium) the peripheral ends are but few; further in numerous Dicotyledons, and species of Smilax and Dioscorea. In the flat leaves of the Dicotyledons the terminating bundles sometimes run along strong (marginally directed) nerves, sometimes they are small short branches which terminate at the margin, and especially in the marginal teeth. It is a phenomenon of especially frequent occurrence that two or more branches, one from each side, unite near to the margin with one stronger, marginally-directed bundle; they then run together outwards to the margin, so that in other words the free ends pass off from the sympodial marginal bundle. This is the case in the leaves of Primula sinensis, Papaver, Brassica, Fuchsia, Calendula, Cucurbita, Mercurialis, and Camellia japonica. The leaves of the Cupuliferæ[1], Betulaceæ, Myrica, Planera, Ulmus, species of Trifolium, Tropæolum, &c. are further examples belonging to the present category, which however have not been exactly investigated as regards the last-mentioned condition. Small branches go from the sympodial marginal branches towards the margin, in the investigated species of Smilax and Dioscorea.

Sect. 92. As regards the arrangement of the bundles as seen in a transverse section of the foliar expansion, they run, of course with the exception of their peripheral ends, within the other tissues, not superficially, those in the ribs being enclosed by the collenchyma and sclerenchyma, or by the aqueous tissue (p. 116), which forms the mass of the projecting rib, or rarely by the chlorophyll-parenchyma, which extends in greater or less bulk into the rib. For those which do not lie in prominent ribs, that is, for the smaller branches of most ramifying bundles, and for all the bundles of many fleshy Monocotyledonous leaves, the *rule* holds, that they lie close within, or below the inner limit of the chlorophyll-containing palisade-cells or rows of cells, which are perpendicular to the surface of the leaf, but are not embedded in that tissue. Thus in the bifacial leaves (comp. Chap. IX) they lie in the spongy parenchyma, where this borders on the palisade layer; in leaves whose tissues are arranged on the centric type, at the periphery of the (colourless) middle layer; in intermediate forms, such as Dianthus Caryophyllus and Crassulaceæ, at the point where the rows of cells which run inwards perpendicularly from the whole leaf-surface meet at the middle of the leaf. In the first and last cases the bundle-system is accordingly extended, in reference to a horizontal leaf, in a horizontal plane, in the second case on the surface of a much-flattened hollow body.

I know of no exceptions to this rule in bifacial leaves. In concentrically constructed expansions with a relatively thin middle layer, consisting only of a few layers of cells, all the bundles are often enclosed within the latter (e. g. leaves of Statice monopetala, Phyllodes of Acacia marginata), or the stronger bundles are within the middle layer, and only the thinner branches at its outer limit (Hakea ceratophylla, Acacia longifolia, Huegelii). In the leaf of Agave americana the thick middle layer is traversed by several series of bundles, which, with the exception of the central ones, stop short towards the margin; they run parallel to the surface of the leaf, and are connected by anastomoses: besides these there is an external series which extends round the whole leaf, at the limit between the chlorophyll layer and the middle layer. In each of the

[1] Von Ettingshausen, Blattsk. d. Dicotylen, Taf. I, II, &c.

longitudinal lamellæ of the thick middle layer of the leaves of Typha and Sparganium, which are separated by large air-cavities, there lie 1–3 longitudinal bundles: numerous smaller ones are placed at the outer limit, abutting on a bundle of hard hypodermal sclerenchyma. In the thick leaves of the Mesembryanthema (M. linguæforme and its allies, M. barbatum, imbricatum, stramineum, &c.) the main branch-bundles run longitudinally through the centre of the middle layer, and send out branches on all sides in an obliquely apical direction, which extend with their reticulately connected ultimate ramifications to its outer limit. Also in the thick leaves of the Crassulaceæ, and even of the Semperviva, divergences of the bundle-branches and meshes are found towards the surfaces: this is most strikingly seen in the branch-bundles which end at the surfaces in the thick-leaved species of Crassula to be described below (Sect. 111).

On the arrangement of the bundles peculiar to the fructiferous leaves of Platycerium, which, from its form, belongs to this category, and upon the peculiarities of vascular bundles in the sporangium-bearing leaves of Ferns generally, which will not be further treated in this work, the Pteridographic literature should be referred to, especially Mettenius, Filices horti Lipsiensis.

It is well known that within all types there is found the greatest variety in the direction of the bundles, and of the corresponding ribs of different orders, in their divergence, number, and relative strength. It is the province of the special description of plants to enter into the details of these conditions of nervation.

The examples of amphibious plants, of leaf-like phyllode branches, of plants with rudimentary leaves and cortical networks of bundles, show that the bundle-system may be immediately dependent upon different adaptations. Sometimes it is altered according to different adaptations of morphologically equivalent members: the submerged leaves of the water Ranunculi and of Elatine Alsinastrum belong to the first type with a separate course of the bundles, while the aerial leaves of the same species belong to the reticulate type: sometimes a similar bundle-system appears in morphologically different members subject to similar adaptation: phylloclades of Myrsiphyllum, and Ruscus, as compared with foliage leaves of allied plants.

On the other hand, the different main and subsidiary forms of the vascular system cannot in most cases be referred directly to adaptative causes. Within a narrower or wider circle of relationship the same type of nervation occurs, whether the adaptation be similar or different, and the converse is also the case. Further the nervation is to a great extent independent of the form of the leaf. After what has been said above it is superfluous to adduce examples of this.

Among the large divisions of the vegetable kingdom the Dicotyledons show the greatest uniformity of ground-plan of nervation, since their aerial foliage leaves, with the one exception of the narrow-leaved Eryngia, all belong to the reticulate type; and individually they show the greatest variety, since in this type variations and combinations of different points of detail are possible, and really exist.

Among the Monocotyledons the great majority of forms belong to the striated type, which shows generally an extraordinary uniformity in the main phenomena. Only the few above enumerated families and genera appear as remarkable exceptions, since some of them correspond exactly to the reticulate type of Dicotyledons, while others approach it.

Among the Gymnosperms Gnetum alone (in accordance with other points in its morphology which approach nearest to the Dicotyledons) has a truly Dicotyledonous nervation: the pinnæ of Stangeria have only single marginal anastomoses: all other forms have bundles with separate course.

The variety of the vascular system in the large foliar expansions of the Ferns is worthy of observation: here even in a narrow circle of relationship, e.g. in the genera Polypodium and Aspidium (in the sense of Mettenius, Fil. hort. Lips.), some species have separate bundles of the most simple arrangement, others reticulate veins; here also there are found sometimes in one and the same species, sometimes especially in different species, all intermediate forms between the most different types. The number of the bundles on a given area is always small in Ferns as compared with Angiospermous Phanerogams, but the plan of their distribution, e.g. in Ophioglossum vulgatum and Platycerium, is often the same as in the reticulated leaves of Dicotyledons.

d. *Connection of the bundle-systems of shoots and branches of different order.*

Sect. 93. The bundle-system of the lateral, similar or dissimilar branches of one relatively leading axis is continuous with that of the latter, and inserts itself upon it. The form in which this is brought about depends in the main upon the morphological quality of the leading and lateral axes, the morphological point of origin of the latter, and the course of the bundles within the axes under consideration. Specific peculiarities are found besides in many cases. According to these relations the following summary may be subdivided thus :—

I. SIMILAR BRANCHES OF LEAFY STEMS.

1. Normal Branches[1].

a. Dicotyledons and Gymnosperms with a ring of bundles.

Sect. 94. The normal branches of the Dicotyledons and Gymnosperms treated in Sect. 61–63 are in the large majority of cases axillary; we shall therefore speak here of these exclusively. There are but few relevant investigations on the rarely occurring extra-axillary branches, some few of which are referred to below.

The primary bundle-system of the axillary lateral shoots, when it consists of leaf-traces, shows four main forms of insertion on that of the leading shoot.

In most cases it unites itself at the point of insertion of the branch into two or a few bundles: these insert themselves, at the node of the leaf which bears the shoot, on those bundles of the trace of the leading shoot which border on the gap of the bundle-ring (gap of the leaf which bears the shoot) formed by the exit of the median bundles of the trace.

In a second, apparently less numerous series of cases, the two or few bundles of the base of the branch enter the ring of bundles of the leading shoot, at the node of the leaf which bears the shoot; they pursue an individual course down to a lower node, and here insert themselves like bundles of the leaf-trace.

In these two cases the arrangement of the bundles of insertion is always such that there is direct continuity between the pith of the leading and lateral shoots.

In a third series of cases the bundle-system of the lateral shoot inserts itself

[1] In the sense of Sachs, Lehrb. p. 174, 2nd Eng. ed. p. 171.

externally, at the node of the leaf which bears it, with numerous bundles, on the many-bundled ring of the leading shoot, so that the pith-cylinders of the shoots of the two orders are only connected by narrow medullary rays.

The fourth category is represented by many Cactaceæ of very peculiar character, to be described below.

A number of instances of the first and second category have been carefully investigated by Nägeli and others who followed him in investigating the course of the primary leaf-traces[1]. In those belonging to the first series, and these are the most numerous, the bundle-system of the axillary shoot is united at the point of insertion into two bundles, which may be called the bundles of insertion. These affix themselves to the bundles of the trace at or immediately below the node of the leaf, which bears the shoot, either—

(*a*) Upon the bundles descending from above, which form the lateral limit of the gap of the leaf which bears the shoot, the one being inserted on the right, the other on the left—Iberis amara, Lupinus (axillary shoots of the cotyledons, Fig. 94, p. 238), Passiflora Vespertilio (axillary tendrils), Antirrhinum majus, Urtica Dodartii, also Pisonia; Juniperus (Fig. 108, p. 246), and the short shoots (the bundles of needles) of Pinus (Fig. 110, p. 247); or (*b*) on the bundle or bundles of the trace of the leaf itself, which bears the shoot—Anagallis arvensis (axillary peduncles), Clematis (p. 245).

In Satureja variegata both the cases designated (*a*) and (*b*) are found to occur. In Galium and Rubia first the two bundles of the trace of the first pair of leaves, and then those of the second pair of leaves of the axillary shoot insert themselves, usually at the node, on the bundle which passes into the leaf bearing the shoot; the same is usually the case in Russelia juncea, and sometimes in Spergula arvensis.

In the second series of cases the two bundles of the axillary shoot pass, at the node of the leaf which bears it, into the bundle-ring of the leading shoot, and pursue an individual course down through one (e. g. Aristolochia, Fig. 96, p. 239, Lathyrus Aphaca, Figs. 98, 99, p. 240), two (e.g. Cerastium frigidum, Figs. 102, 103, p. 243), and even three internodes (e. g. axillary peduncles of Viola elatior), and then insert themselves on bundles of the leaf-trace. For further examples and details, see Nägeli, *l. c.*, and above, Sect. 61, p. 235. In the species of Galium, Rubia, Spergula, and Russelia above enumerated there is, according to Nägeli, either direct insertion at the node of the leaf which bears the shoot, or the bundles pursue an individual course down through one internode or more. In Vitis vinifera usually three bundles pass from the axillary shoot, and also from the extra-axillary tendril into the main shoot, and pursue a separate course through one internode.

The two or three bundles of insertion of the axillary shoot arise either by the coalescence of the several bundles of the leaf-trace of the lowest internode to two at the point of insertion, e. g. Clematis; or these are the single bundles of the trace of the two lowest leaves, e. g. Galium.

The connection of the axillary bundle-system with that of the leading shoot is however not limited to the bundles of insertion above described. According to Frank's investigations[2] on Taxus, Quercus, Bidens, and Solidago, there appear con-

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[1] Compare above, § 61.

[2] Botan. Zeitg. 1864, pp. 154 and 382.

necting bundles, one in Quercus, in Taxus about three, which run down from the upper margin of the gap of the leaf-bearing shoot to the bundles of insertion. By means of these and further 'completing bundles' the point of connection of the pith of the main and axillary shoots is soon enclosed by a ring. The completing bundles doubtless belong to the secondary formations of intercalary bundles (Chap. XIV); the same is probable for the above connecting bundles, but their relation to the leaf-traces of the axillary shoot requires more exact investigation.

As regards the insertion of the bundles of axillary shoots, two or more of which are seated one above another, Frank's statements may here be reproduced word for word (*l. c.* p. 388), but the subject is recommended for further research. 'In Rubus two buds are seated in the axil of the leaf closely one above another, their vascular bundle-systems are united in the lower parts one with another, and are connected with the vascular system of the stem as though they belonged to one single axillary bud. After both lateral series (i. e. the branches of the two original bundles of insertion, De Bary) have united at their anterior ends (i. e. next the leaf which bears the shoot) each separates at the middle, and the anterior halves close up to form a circular system for the lower bud. The remaining posterior halves soon unite at their anterior ends and form the vascular bundle-system of the upper bud. The posterior parts of both circles of vascular bundles are here also closed by descending bundles, which accordingly arise in the case of the lower bud from the vascular bundles of the upper.—In the axillary buds of Lonicera Xylosteum, of which often as many as four are seated one above another, but which are usually separated some distance one from another, and the uppermost of which can hardly be distinguished externally from an adventitious bud, the lower parts of the vascular bundle-systems are also inserted between the members of the vascular bundle-ring of the stem, but in this case each system is independently connected with the stem, since the gap of the vascular bundle-ring of the mother shoot closes above each bud, and only opens again immediately below the insertion of the next, at which point the bundles of the bud arise on both sides from the margins of the open vascular bundle-ring.'

The third, less common case of insertion of the axillary bundles outside the closed bundle-ring of the leading shoot occurs in the Umbelliferæ, though not in all of them. The bundles of the leaf-trace of the lowest internode of the axillary shoot unite in this case at the node of the leaf which bears the shoot, to form one cortical bundle, which immediately divides into two arms; these pass off right and left, and embrace the bundle-ring of the leading shoot transversely like a girdle. From this girdle branches arise in pairs side by side and pass downwards. Each of these pairs bestrides one bundle of the trace of the leaf, which bears it, from above and outside, and inserts itself on its two sides, at the point where it curves outwards from the bundle-rings of the leading shoot. The bundle-system of the axillary shoot is thus attached outside the ring of the stem by the pairs which bestride the same number of emerging bundles of the leaf which bears it. It thus embraces either the whole circumference of the node, bestriding all the emerging bundles of the stem-embracing trace of the leaf which bears it—Fœniculum, species of Heracleum, Chærophyllum, Myrrhis, and Archangelica; or a part of it bestriding only some few bundles of the leaf which bears it—Æthusa Cynapium. A continuity of pith between the shoots of both orders is thus only possible by the narrow medullary rays.

The phenomenon stands thus in the mature plant[1]. The exact study of the

[1] If I am not mistaken, it has been long ago described by C. F. Schimper as 'Astkorb;' I have not succeeded in my attempts to find the reference.

history of development remains still to be made. The arrangement can still be recognised after considerable secondary thickening of the stem; the stem-embracing insertions of the branches which are thick, but attached by thin bases, weave in a basket-like manner round the node of the leading axis: it is especially developed in the perennial subterranean shoots of Myrrhis, species of Chærophyllum, &c.

Many Umbelliferæ have, as is obvious from the continuity of the pith-cylinder on both sides, another form of axillary insertion, which remains to be more exactly investigated: thus Silaus pratensis with its medullary bundles noticed on p. 253.

The same form of axillary insertion as in the above-named Umbelliferæ is found in Aralia japonica; it remains to be investigated whether the same is the case in other Araliaceæ, and in other families in which the leaf-insertion, and perhaps also the bundle-system, resembles that of the Umbelliferæ, e. g. Ranunculaceæ with alternating leaves.

The above-mentioned fourth, and very special case of bud-insertion occurs in species of Echinocactus, and some of Cereus with thick shoots (C. candicans?). Its development requires investigation. In the mature state the leaf-traces having one bundle are found united to form sympodial bundles, which are separate and perpendicular, and of equal number to the angles of the stem (Echinocactus), or are connected in a reticulate manner; between them are broad medullary rays. The leaf-bundles run slightly obliquely, almost horizontally upwards towards the lower margin of the spine-cushion, that is towards the point of insertion of the rudimentary leaves. Just above each foliar-bundle and in a direction almost parallel to it, the thick cortex of the stem is traversed by some few vascular bundles, which are near one another, and have their xylem-portions turned towards one another; these belong to the axillary bud formed above the rudimentary leaf, and attain a considerable strength as soon as the bud developes into a shoot. These bundles of the bud now pass through the medullary rays, between the sympodia of the leaf-trace in the stem, into the pith, and there branch freely in all directions, their branches being united one with another to form an elaborate plexus traversing the whole pith. This system of bundles of the bud is only directly connected with the sympodia of the leaf-trace by single short connecting bundles at the points of passage through the medullary rays. In the Opuntias, Cereus speciosissimus, &c., and also in the Rhipsalidaceæ[1] this phenomenon is wanting; the bundles of the bud, as far as investigated, are inserted, in the manner usual for Dicotyledons, partly on the cortical bundles, partly on those of the bundle-ring: medullary bundles are altogether wanting. In the Mamillarias, which have medullary bundles (p. 254), no connection between these and the young lateral shoots has as yet been discovered.

The above-named plants have accordingly a system of medullary bundles, which differs fundamentally in its significance from the others described above on p. 253.

Where these latter, and where cortical bundles occur in Dicotyledons, the axillary insertion occurs, as far as is known, in one (usually the first) of the typical forms, with the addition of direct connection between the medullary or cortical bundles of the leading shoot and of the lateral shoot.

[1] Compare Vöchting, *l. c.* (p. 261).

b. Monocotyledons and Phanerogams with axile bundle.

Sect. 95. Among the Monocotyledons belonging to the Palm-type (Sect. 65–67) the numerous bundles of the lowest internode of the normal axillary shoot enter, in the Palms[1], Dracænas, Liliaceæ, Aroideæ, Orchidaceæ, &c., at the node into the bundle-cylinder of the main shoot, and pass obliquely downwards and inwards with the bundles of the leaf which bears the shoot, inserting themselves successively on peripheral bundles of the latter, without reaching the middle of the cylinder. In many cases, as in the rhizomes of Acorus, the axillary bundles do not penetrate further than to the surface of the cylinder of the main shoot, but spread themselves out, with abundant branching, for a great distance downwards, over the nearer longitudinal half of the main shoot, and interweaving, and here and there uniting with the bundles at the surface of the cylinder, they form a dense plexus of bundles, which is sharply limited on the side next the cortex.

In those forms which have been investigated, Zea, Saccharum, Coix, Arundo Donax, &c., numerous bundles pass from the lowest internode of the axillary shoot transversely into the node, and here branch very freely, their branches spreading over the whole transverse section of the node, but only slightly in a vertical direction, and thrusting themselves between the bundles of the main axis, which run perpendicularly through the node, and between one another, and here and there inserting themselves on the bundles of the main axis. The whole series of axillary bundles forms at the node a complex and confused felt, expanded and attached in the manner indicated, and having the form of a transverse disc, which in the above-named large species reaches a height of several millimetres[2]; its origin is not obvious in the mature state, but it is clearly seen in young stages of development that it is formed by the insertion of bundles, starting from the axillary shoot.

In the Commelineæ with thin stems, as Tradescantia albiflora, Commelina agraria, several internal bundles are found in the basal internode of the young axillary shoot (comp. Sect. 69)—e. g. three or four in the Tradescantia named—which enter the node of the main shoot, and here, turning downwards above the outgoing median bundle of the leaf which bears the shoot, insert themselves at the point of union of the inner bundles. In somewhat older axillary shoots there are further peripheral, doubtless in part cauline bundles, which insert themselves on the cauline bundles of the main shoot. In thick stemmed Commelineæ, such as Maravelia zeylanica and species of Dichorisandra, the internal bundles of the lowest internode of the axillary shoot unite to a single thick bundle, which passes almost exactly horizontally into the node of the leaf which bears it, and inserts itself in the middle of this, with some few branches, on the internal bundles which descend there. In Tradescantia virginiana several bundles pass from the axillary shoot into the node of the leaf which bears it, and there divide into branches, which are interwoven as in the nodes of the Grasses between the internal bundles of the main shoot, and insert themselves on them.

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[1] Mohl, Palm. Struct. p. 31.—Compare also Falkenberg, *l. c.*, and the note above on p. 276.

[2] Compare von Mohl, *l. c.* Tab. 9; Schleiden, Grundz. 3 Aufl. II. p. 158.

In the node of Potamogeton natans the bundle-system of the young axillary shoot coalesces so as to form a single bundle, which inserts itself on the median bundle of the leaf which bears it, at the point where it curves outwards. The other investigated Potamogetons—P. lucens, gramineus, pectinatus, and pusillus—show a quite similar insertion, with the difference that the bundle which comes from the axillary shoot is not inserted on the bundle passing into the leaf which bears it, but on the axile sympodial bundle which passes downwards at the node. Comp. Fig. 123, p. 273.

As far as is known, the naturally very simple relations of insertion in those Phanerogams which have an axile bundle resemble those in the last-named Monocotyledons.

c. Fern-like plants.

Sect. 96. Among the Filicineæ there is sometimes forked, sometimes Monopodial branching; in many species, as in Aspidium Filix mas, Athyrium Filix fœmina, both forms of branching are found side by side.

Monopodial branching occurs undoubtedly in the *Salviniaceæ*, *Marsiliaceæ*, and in many *Filices*. Very many Filices show a shoot-system, apparently composed of a main axis and lateral shoots, in respect of which it is a matter of controversy whether it is a Monopodium, or a Sympodium composed of unequally developed successive forks. It will here be treated as a Monopodium, in accordance with the conclusion of Mettenius. But I remark distinctly that I only accept this conclusion in order to simplify the description *here* to be given, and that I leave the controversy in question quite undecided. The fact that the insertion of the bundles of the actual lateral shoots appears in many cases in point to support the conclusion of Mettenius cannot by any means decide the question, since unequally strong growth of originally equivalent shoots may also have as its result an originally unequal arrangement of their vascular bundle-system.

The normal lateral shoots of the plants of this series, with the exception of many Hymenophyllums and Davallias, which in this point also are the subject of controversy, are not axillary, nor have they even any other constant relation to the insertions of the leaves.

They arise either from the stem, and sometimes close to the point of insertion of the leaf, laterally or at the back of the latter, sometimes at a great distance from it, between two leaves; or they arise on the back or sides of the base of the petiole itself, often, as in the ordinary branchings of Aspidium Filix mas, which may be accordingly considered as belonging here, at a considerable distance from the point of insertion, in the above-named example about 2–3 centimetres from it. Comp. Fig. 132, C, p. 286.

In the undoubtedly Monopodial branching of many Filices with more than two rows of leaves, the vascular bundle-system of the lateral shoot is united as a rule towards the point of origin to one thin and not hollow bundle, which is inserted on one bundle of the main axis. This is the case in the lateral shoots of Aspidium cristatum, spinulosum, Blechnum Spicant, Athyrium Filix fœmina, Polypodium alpestre, Alsophila aculeata, &c.[1], which appear at or below the back of the base of the

[1] Hofmeister, Beitr. *l.c.*—Stenzel, *l.c.*; compare p. 283.

petiole. The single thread-like bundle, which enters the narrow base of the branch, is inserted, in the first-named plants, at the lower margin of a foliar gap of the stem; in the specimen of Alsophila investigated several bundles are thus inserted, each of which passes into one of the numerous shoots which arise round the base of one leaf. The bundle of the lateral shoot of Struthiopteris has the same point of attachment as in Aspidium cristatum; it is not thread-like, but has the shape of a plate with a channel-like external groove, which gradually widens as it passes from the point of attachment, and closes up to form a tube opening obliquely outwards and downwards. Through the tube and channel the pith of the lateral shoot has continuous connection with the parenchyma of the main shoot, while where the bundles are filiform at their point of origin this continuity does not exist. The lateral shoots seated on the petiole in Aspidium Filix mas have as a rule the same thread-like insertion of the bundles on one bundle of the petiole. More rarely the bundle-system of the lateral shoot arises as three bundles from so many bundles of the petiole, or directly as a tube filled with pith from the margin of a gap in a widened band-like bundle of the leaf. Finally, in a species named as Diplazium giganteum, Stenzel found this latter form of insertion in the branchings arising from the stem below the leaves: each branch has its own small gap in the network of bundles of the stem, from the margin of which arises the tube-like system of the branch.

In the Ferns and Rhizocarps with elongated stems bearing two rows of leaves, and with lateral shoots arising from the stem, not from the petiole, when there is a simple axile bundle present, there is naturally an insertion of the bundle which passes to the lateral shoot on that which traverses the main shoot. In the Marsiliaceæ with a tubular bundle, that which enters the branch passes directly off in a tubular form from the margin of a corresponding gap in the tubular bundle of the main axis, through which gap the pith of the two axes is continuous.

In the Ferns with clearly marked upper and lower bundles (see above, p. 287), in most of the described cases[1], the bundle-system of the lateral shoot is united, as in those ferns with leaves in many rows, into one bundle, which arises from the next lower transverse bundle separating the foliar gaps: it usually has the form of a channel open towards the pith. This is the case in Aspidium albopunctatum, coriaceum (comp. Fig. 135, p. 287), Acrostichum Lingua, brevipes, most Davallias, and other above-named species, on the details of which Mettenius' description must be referred to. According to Trécul's investigation[2], however, it appears that in A. coriaceum the bundle passing to the branch is inserted both on the transverse and on the lower bundle, at the angle between the two. Among the Davallias some species (D. stenocarpa, divaricata) differ from the rest, inasmuch as a closed transverse bundle limiting the foliar gaps is absent, but in its place, and in the direction which it has in other species, two bundles run, the one arising from the upper, the other from the lower bundle; both converge obliquely towards the apex, and enter the lateral shoot as upper and lower bundles without coming into contact. The arrangement in D. chærophylla described by Mettenius is more irregular still, but should be placed in this category.

[1] Mettenius, Angiopteris, p. 546.

[2] Ann. Sci. Nat. 5 sér. tom. XII. p. 242.

Of the Ferns with divided upper and lower bundles, which are connected by intermediate forms with those above described, and with those in which there is only a complex, often irregular network of bundles instead of two bundles (see p. 288), this only may be stated generally, that in many simply constructed forms, e. g. Polypodium squamulosum, the bundle-system of the lateral shoots arises as a simple bundle from a definite mesh in that of the main axis. In the large majority of these cases several thin bundles, which enter the lateral shoot, arise from the margin of definite meshes (comp. Fig. 136, p. 287). Their number varies according to the species, from two to eight, as far as present data extend, and is always smaller than that which enters a leaf of the same species. Where medullary bundles are present, and there is continuity between the pith of the main and lateral shoot, branches separate from the medullary bundles of the former and enter the latter, e. g. Polybotrya Meyeriana; where the bundles of the lateral shoots insert themselves as a simple not hollow bundle, such a branching does not occur.

When the lateral shoots arise from the base of the leaf, modes of insertion of bundles are found which are similar and subject to similar variations to those of the bundles arising from the stem: this is shown by the above-mentioned example of Aspidium Filix mas. There are but few thorough investigations on this point.

No exact investigations have been made either on the insertion of the bundles at the rarely occurring points of branching of the Osmundaceæ, or on the mode of origin of these branchings.

In the Equiseta the bundle-system of each branch is united into a single bundle, and inserts itself externally at the node of the main shoot on the angle of branching of one of the bundles descending from the next higher leaf-sheath (comp. p. 279)[1].

Where the branching appears and remains as a forking of the main axis, the whole bundle-system also divides into two parts, each of which enters into one branch of the fork: both systems are fundamentally similar to one another and to that of the main axis.

Among Ferns the rhizomes of Pteris aquilina[2] are—if we disregard for the present the above-mentioned controversies—an exquisite example of this. Comp. Fig. 143, p. 295. Also in Athyrium Filix fœmina, according to Hofmeister, the phenomenon is frequent; in Aspid. Filix mas it is rare; these cases are regarded, it is true, by Mettenius as an apparent forking, derived from early stronger development of monopodially formed lateral shoots.

In the Lycopodia and Selaginellæ, whose branchings are always forked—though not always quite equal—the insertion of the vascular bundles which enter the branches is generally indicated by what has been said above. In the Selaginellæ with two lateral bundles in each shoot, as in S. Kraussiana, Martensii, &c. (comp. p. 282), of the four bundles destined for each branching either three diverge acutely from one bundle of the main shoot, and the fourth is the continuation of the other which traverses the main shoot; or each of the latter divides into two branches which are very close to one another at their entry into the fork. In S. Martensii the former

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[1] See Stenzel, *l. c.* Taf. IV. Fig. 13.

[2] Compare Hofmeister, Stenzel, *ll. cc.*

case has been observed[1], in S. Kraussiana[2] both cases are found; in the latter there is also a more or less complete transverse anastomosis at the point of branching. The passage into the lateral shoots has not been exactly investigated in those Selaginellæ which have several bundles in their shoots.

2. Adventitious Shoots.

Sect. 97. It is a general rule for adventitious shoots that their bundle-system is always inserted on those vascular bundles, or points of the wood or bast body of the main axis, which are nearest to their point of origin. Since such shoots may arise at the most heterogeneous points, and at the most various periods of the life of the plant, the individual cases show great variety. If the normal course of the bundles is known, their relative arrangement is completely determined by what has been said above.

II. ROOTS.

Sect. 98. In the forked roots of the Isoeteæ, Selaginellæ, and Lycopodia, the vascular bundle forks as in dichotomous stems.

Roots are found as lateral branches on members of their own kind, as well as on stems, rarely on leaves[3]; some appear in definite morphological positions, e. g. at definite points of the leaf-insertion; others are without arrangement: the former may be called normal, the latter adventitious lateral roots.

The invariably endogenous formation of lateral roots takes place in or close to vascular bundles or masses of wood or bast. Their vascular bundle is inserted directly and without branching on the nearest one of the main axis, or it divides into branches, which connect themselves with several bundles of the axis.

The former simple insertion occurs obviously in members with a simple axile bundle—thus in almost all roots; also in stems constructed on the Dicotyledonous type, and in the Ferns.

Splitting of the bundle of the root into several shanks, which insert themselves on several bundles, is a common phenomenon in the stem of Monocotyledons. It does not occur however in all species; e. g. in the rhizome of Carex hirta each root-bundle inserts itself simply on one peripheral bundle of the stem-cylinder.

The branches or shanks, into which the root-bundles about to be inserted are divided, separate at the periphery of the bundle-cylinder, they then insert themselves, in a first series of cases on the bundles which are present at that point, without penetrating more deeply into the cylinder of the stem: this is the case in the investigated Orchideæ, many Commelineæ, Aroideæ, Richardia æthiopica, Philodendron spec., with few short shanks, diverging chiefly upwards and downwards; Acorus with more abundant branching; Calla palustris[4] with a ring of roots, whose bundle-insertions together form a transverse girdle at each node of the rhizome.

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[1] Compare Nägeli und Leitgeb, Entstehung, &c. d. Wurzeln, Taf. XVIII. Fig. 11.

[2] Hofmeister, Vergl. Unter. Taf. XXIII. p. 4.

[3] [Compare Mangin, Origine et Insertion des racines adventives . . . chez les Monocotylédones, Ann. Sci. Nat. sér. 6, tom. 14, 1882.]

[4] Van Tieghem, Struct. des Aroidées, *l. c.*

In another series of cases the bundle of the root divides at the outer limit of the stem-cylinder into numerous branches, which, diverging in all directions, enter between the bundles of the stem, and penetrate with a sinuous course to the middle of it, and then insert themselves, some of them further out, others further within, on bundles of the stem. This is the case in the Palms [1], where the penetrating bundles do not reach the middle of the stem, in the nodes of the Grasses, and thick-stemmed Commelineæ.

Also in the thick primary lateral roots of Pandanus the bundle-system of the corresponding lateral axis inserts itself on that of the main axis in the manner just described, i. e. numerous radiately diverging and undulating branches pass between and up to the longitudinal bundles, which will be described below (Sect. 108): also in the Palms, according to Mohl, the bundle of the lateral roots splits in a similar way into thin branches, and penetrates between the elements of the hollow cylindrical bundle of that which is relatively the main root.

The phenomena in the above Commelineæ should be rather more exactly described. Several lateral roots arise at the nodes, especially on the side opposite to the axillary shoot, and somewhat higher than its point of insertion, and the point of union of the bundles of the leaf-trace. The bundles of the latter penetrate horizontally into the stem as far as the cylindrical surface occupied by the ring of cauline bundles (see p. 269). Here they divide into horizontally diverging shanks, and these together form a slight transverse girdle passing round the whole periphery. In the thin stems of Tradescantia albiflora and Commelina agraria this girdle is without centripetal branches. In Tr. zebrina, virginiana, and Maravelia zeylanica numerous branches pass down from it in a centripetal direction, they are distributed transversely through the whole node, with sinuous curvatures, and anastomose with the descending bundles of the stem, and with those which enter from the axillary shoot, thus forming a felt, which is less dense and deep than that which is characteristic of the nodes of Grasses, but is similar to it.

B. STRUCTURE OF THE VASCULAR BUNDLE.

Sect. 99. The vascular bundles are strands which consist of tracheæ and sieve-tubes as their essential parts. Both are accompanied by parenchymatous, and often by sclerenchymatous elements. The structure of the bundle is determined by the juxtaposition of all these component parts.

A bundle undergoes in its course more or less considerable changes. Cross-sections of the same bundle, taken at a distance from one another, may show the greatest differences in the number and distribution of the individual elements; Fig. 147, for example, represents the part of a bundle of the leaf-trace of Acorus Calamus passing through the leaf, while Fig. 148 shows its lower end as existing in the stem; in the intermediate tract the one structure passes gradually over into the other. Such differences come out most conspicuously on comparing the peripheral ends of the bundles, where they are spread out in the leaves or periphery of the stem, with the other parts of them. It is therefore expedient in considering them to distinguish

[1] Von Mohl, Palm. Struct. p. xix. Tab. I. A, and Verm. Schr. pp. 157 and 172.

between *bundle-ends* and *bundle-trunks*, although a sharp limit between the two cannot be shown in any case.

To the category of *bundle-trunks* belong chiefly the bundles which pass through the stem, roots, leaf-stalks, and thick nerves of the leaf. The description of their structure must start from these organs.

Most bundle-trunks, however different in details, possess the composition which has above been indicated in a general way. In comparatively few cases their structure is simplified by essential organs disappearing or remaining rudimentary. A distinction must therefore be drawn between *incomplete* and *complete* bundle-trunks. Here we shall first speak of the latter.

I. Bundle-trunks.

Sect. 100. The essential tissue-elements of the complete bundle are tracheæ and sieve-tubes. The two are always so arranged that one longitudinal portion of

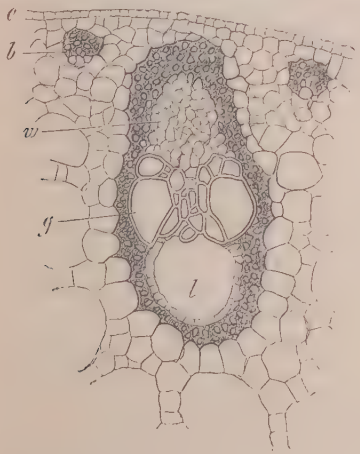

Fig. 147.—Acorus Calamus; cross-section through the periphery of the flower-stalk (145). *e* epidermis; *b* small vascular bundles, with a sclerenchymatous sheath on the outside. In the middle is a large vascular bundle; *w* its phloem; *g* outer large tracheæ of the xylem; *l* intercellular passage at the inner side of the latter. The cross-section through the leaf shows the same structure.

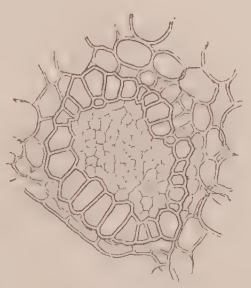

Fig. 148.—Cross-section through the concentrically arranged lower end of a bundle of the leaf-trace in the stem (145). The delicate and small-meshed phloem occupies the middle, and is surrounded by a ring of scalariform netted tracheides; outside this is parenchyma.

the bundle includes all the tracheæ, while another, or in rarer cases more than one other, includes all the sieve-tubes. Thus in every bundle we have to distinguish between that part which contains the tracheæ (tracheides or vessels) and that which contains the sieve-tubes, or expressed more shortly, between the *xylem* and the *phloem*.

In both parts the characteristic tissue-elements are as a rule not present alone, but are placed between rows or layers of cells (cf. p. 5) in such a way that all or most tracheæ or sieve-tubes are in contact with the latter at least at one point. It is true that in the case of very small bundles this intercalation is not uncommonly absent in the xylem; but then the few tracheæ of which this consists, border, for the most part at least, on the cells which encircle the bundle. More rarely masses of

tracheæ, consisting of several or many rows as seen in cross-section, without intercalated cells, occur in the xylem of thick bundles, as in the Marattiaceæ, Osmundaceæ, and Ophioglosseæ[1], and in the bundles of the leaf of Yucca, the stem of Fritillaria[2], &c., to be described below.

The external surface of a vascular bundle is marked off from the surrounding non-equivalent tissue in various ways, and not uncommonly in such a manner that the surrounding parenchymatous elements pass over directly and quite gradually into those which lie within the bundle itself, between the tracheæ and the sieve-tubes. A smooth, sharp, external boundary is then not present at all, although the bundle itself, in so far as it consists of its essential elements, always stands out sharply. More frequent no doubt is the complete or partial limitation of the bundle by means of a distinct sheath, strand-sheath, or bundle-sheath[3], in the sense of the word fixed in general at p. 6. This occurs, firstly, in the form of the endodermis (p. 121), or other specialised parenchymatous layers (Chap. IX); secondly, in the form of strands or layers of sclerotic fibrous cells, or especially sclerenchymatous fibres, which border the bundle on one side or encircle it all round. All these sheaths are as a rule limited on the inside towards the bundle with the same sharpness as on the outside towards the non-equivalent surrounding mass; they can therefore just as well be assigned to the bundle itself as to its surroundings, its boundary being fixed either at the external or internal surface of the sheath. The latter is the usual and expedient practice in the case of parenchymatous, and particularly of endodermal sheaths, especially on the ground of developmental phenomena in almost all roots; yet it must not be left out of consideration that in the case of the endodermis of most bundles in Fern-stems the history of development rather leads to the opposite result. Cf. Sect. 106.

As regards the sclerenchymatous strands and sheaths which accompany the bundle longitudinally, it has long been customary to assign them to the vascular bundles, or, as was done by Nägeli, to regard them at least as essential concomitants of the latter, and to call the united strand formed by them and the vascular bundle the fibro-vascular strand. Both from former sections, and further from the general comparative consideration of the distribution of sclerenchyma (Chap. X), it follows that these fibrous sheaths and strands do not strictly speaking belong to the vascular bundles, but to a special system of tissue, which may or may not have a common course with the latter over certain tracts.

In spite of all these theoretical considerations, the anatomical treatment of the vascular bundles cannot by any means leave sheaths of whatever kind unregarded where they occur.

The elements of the vascular bundle are, as far as investigations reach, almost everywhere and always in uninterrupted connexion, both among themselves and with those of the surrounding sheaths. The only not uncommon exceptions are that the xylem, especially in collateral bundles, shows intercellular spaces containing air at its inner edge, and that spaces containing secretions lie in the outer regions of the bundle. Cf. Chap. XIII.

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[1] Compare Russow, Vergl. Unters. p. 117.

[2] Von Mohl, Palm. Struct. Tab. G. Fig. 11.

[3] C. H. Schultz, Die Cyclose, *l.c.* (p. 192) p. 246.—Sachs, Textbook (2nd Eng. ed.), p. 124.—Compare also Russow, Vergl. Untersuch.

According to the arrangement of the xylem and phloem, three main forms of bundles are to be distinguished, which are designated the *collateral*[1], the *concentric*, and the *radial*. One and the same bundle may at different points of its course pass over from one to the other of these forms (cf. Fig. 147, 148).

1. *Collateral Vascular Bundles.*

Sect. 101. Collateral bundles are with rare exceptions characteristic of the stem and foliage-leaves of the Phanerogams, also of the stem of Equiseta, Ophioglosseæ, Osmunda, and Todea (?)[2]. Among parts belonging to the category of roots they occur only in the tuberously developed roots of Dioscoreæ (D. Batatas), Ophrydeæ, and perhaps those species of Sedum which are related to S. Telephium. Cf. p. 233.

In the most numerous and the typical cases they consist of a xylem and phloem portion, each of which borders longitudinally on the other with one surface, and with the remainder of its periphery on the non-equivalent surrounding tissue. A special subordinate form, to be called the double collateral or *bicollateral*, is distinguished from the usual one by the fact that two phloem groups lie on opposite sides of one xylem group. These will be described last, and at present only the simple collateral bundles will be discussed.

The orientation of collateral bundles is in the usual cases, which we may call normal, always such that the xylem is turned towards the middle, and the phloem towards the periphery of the whole organ to which they belong. Accordingly we can use the terms inside and outside as regards the bundle in a general sense, calling the edge turned away from the phloem the inner edge, and using corresponding words for the remaining sides. In the bundle-ring of the typically constructed Dicotyledons and Gymnosperms (p. 235) all the xylem portions lie, in consequence of the orientation mentioned, in an annular zone which immediately surrounds the pith, while all the phloem portions occupy a zone concentric with the former and external to it. The former, together with what is added later by secondary new-formation, is traditionally known as the woody ring or woody mass, the second as the *bast*, *bast-ring*, *bast-zone* or *inner cortex*, and the two parts of the bundle are accordingly called the *woody-part*, and the *bast-part* or *cortical-part*—*xylem* and *phloem*[3], the nomenclature originally adopted for the Dicotyledons being extended to the structurally similar parts of all vascular bundles, without regard to arrangement and orientation. The same orientation is also the rule for the stems of Monocotyledons, and for all leaves or portions of leaves in which the bundles are placed in a ring around a central part from which they are absent. Where on the other hand the bundles in a leaf, or portion of a leaf, have an arrangement other than the annular one just mentioned, their phloem is turned towards the morphologically lower leaf-surface, and their xylem towards the upper, thus preserving the same orientation as in the stem if referred to the latter, the leaf being supposed to be in the erect position.

As regards Dicotyledons with the typical single ring of bundles, no exceptions to these rules are known, unless perhaps in species of Strychnos (cf. Chap. XVI).

[1] Russow, Vergl. Unters.

[2] [Compare Haberlandt on collateral bundles in the leaves of Ferns, Bot. Ztg. 1881, p. 467; idem, 1882, p. 217.]

[3] Nägeli, Beitr. I.

In stems, leaf-stalks, and leaf-ribs with several concentric rings of bundles, or bundles scattered in cross-section, exceptions certainly occur, though rarely; also very rarely in the lamina of flat leaves.

In the positions first mentioned precisely the opposite orientation to that in the normal case is shown by certain bundles in the stem of Nelumbium (Fig. 112, p. 255), namely by those of circles 3 and 5 in the intermediate series; further by the medullary bundles in the stem of the Araliæ mentioned on p. 253, by the four cortical bundles in the internode of Calycanthus, by those of the middle one of the three concentric bundle-circles in the leaf-stalk of the Lime [1], and several others.

In stems and leaf-stalks many bundles which are scattered as seen in cross-section have an *irregular* orientation, i. e. with the two parts facing neither directly outwards nor directly inwards. Those especially which anastomose or branch often show torsions which divert them from the normal orientation, near the points of branching or of union. Examples of this are found in many leaf-stalks, e. g. Aralia japonica, Aroideæ; in the pith of Silaus and other Umbelliferæ mentioned at p. 253; and in the interior of the stem of Aroideæ and Pandaneæ (cf. p. 268).

In the leaves of Typha and Agave Americana (p. 305) the bundles running through the middle layer, which is destitute of chlorophyll, all have their vascular part turned towards the upper side; in those on each side which border on the chlorophyll-parenchyma the vascular part faces the middle of the leaf. Of the longitudinal bundles lying in one plane in the leaf-lamina of Dracæna reflexa, the median one has normal orientation, while all the rest have their xylem turned towards this, and their phloem towards the edge of the leaf.

The general form of the cross-section of collateral bundles is as a rule round or oblong; in the latter case the greater diameter passes as a rule through the middle of the outer and inner edges. In the stems and leaves of several Monocotyledons this unequal extension on different radii of the cross-section amounts to a marked lateral flattening of the bundle; e. g. leaves of Scitamineæ, Asphodelus luteus, Hemerocallis, Hyacinthus, Pandanus, leafy-stem of Canna, &c. Other shapes are rare; such as the horseshoe-shaped cross-section of the bundles in the stem of Osmunda (Fig. 128, p. 280), the annular section in the stem of Botrychium (p. 284), and in the petioles and ribs of several Dicotyledonous leaves, as those of Eriobotrya japonica, Veronica speciosa [2], the pulvinus of the leaf-stalk of Mimosa pudica, &c. In these latter cases the inner edge of the ring is always the inner edge of the bundle, not only as regards orientation, but also as regards structure.

Ignoring these annular bundles, and ignoring the places where several bundles meet, which we shall describe below, both the whole collateral bundle and each of its two parts form an approximately, though never exactly monosymmetrical body, with its plane of symmetry passing through the middle of its outer and inner edges. The arrangement of the elements in the bundle is also in harmony with this approximate monosymmetry, as will be shown below.

The number of elements in each part, and the resulting thickness of the bundle, is extremely different according to the individual cases: many sappy herbaceous

[1] Compare Frank, Botan. Zeitg. 1864, p. 381.

[2] Areschoug, Om bladets inre byggnad. Lund's Univ. Arskrift, tom. IV.

plants, especially Monocotyledons, and water and bog-plants, have only a group of a few (3–6) tracheæ, and a phloem portion limited to about 20 or fewer elements; in the stems and leaf-stalks of many Aroideæ the number of the tracheæ falls in many bundles to 2 and 1[1]; on the other hand, the thicker bundles of Monocotyledonous plants, and above all the thick bundles of the Ferns above mentioned, and of the leaves of Dicotyledonous land-plants, present very high figures. It is an obvious *a priori* conjecture that a definite ratio exists between the size of the bundles, especially of their vascular parts, and their number, and that both are definitely related to the extent of the transpiring and assimilating leaf-surface, as well as to the vigour of the root system and the arrangement of the roots. A number of facts, which have partly been stated here, partly in Sects. 61–71, and are still to be considered in Chap. XIV, point to such relations. The comparison of nearly-related species inhabiting the water and the land respectively, demonstrates among the former a considerable diminution in the development of the bundles (cf. e. g. Figs. 153 and 154), which may extend to the entire disappearance of the xylem. A sufficient basis, however, for the attainment of general results, available for more than individual phenomena, is still wanting, so that we can here only point out these manifest relations without entering into them more minutely.

The structure of the two parts of the bundle, in so far as it is brought about by the juxtaposition of the different sorts of tissue, and by their peculiarities, as described in former chapters, will in the case of the Osmundaceæ and Marattiaceæ be mentioned further on, under the head of concentric bundles in Ferns (Sect. 106). In the other collateral bundles, especially those of the Phanerogams when they consist of more than one or two elements,—

(*a*) The *xylem* is built up of tracheæ and (parenchymatous) cells. At its inner edge lie a few narrow, spirally or annularly thickened tracheæ, which are the first products of the differentiation of the tissues, and are thus to be called primitive elements (Protoxylem of Russow). For the reasons given at p. 157 it is especially these primitive elements in which, in the mature plants, the spiral threads are steeply wound or quite distorted, and the rings widely and often irregularly separated from one another. The primitive elements themselves are not uncommonly compressed by the expansion of their neighbours, and here and there manifestly destroyed. In the Coniferæ, Equiseta, and Ophioglosseæ, the primitive elements are tracheides; the same may be the case in the plants or parts of plants mentioned above at p. 165 as wholly destitute of vessels. In the other cases they are called vessels, and in most instances no doubt rightly so, although just as in the case of the primitive tracheæ, few very accurate investigations of this really not very essential distinction have been undertaken. Outside the primitive elements wider tracheæ follow, which are tracheides or vessels according to the individual cases mentioned in Chap. IV, and especially in Sect. 40[2]. Their development takes place successively, advancing from the inner edge of the bundle outwards, and as a rule at a time when the elongation of the entire part to which they belong is nearly at an end. The thickenings on their walls therefore have a successively denser arrangement: dense spiral and annular tracheæ, then reticulated and pitted tracheæ follow

[1] Compare van Tieghem, Struct. des Aroidées, *l. c.*

[2] Compare details in Caspary, *l. c.*

one another in succession from within outwards, with gradual transitions, or with the omission of one or the other intermediate form. As regards the occurrence of particular forms of thickening, it may at any rate be given as a rule that among the Monocotyledons the series ends with the development of dense fibrous thickenings, annular and spiral fibres, reticular fibres, and surfaces with non-bordered pits or scalariform markings (pp. 158, 163). Bordered pits or scalariform slits here only occur in the collateral bundles of stems which are long-lived and relatively slow-growing, as those of many Palms, and Arundo Donax, and many rhizomes. The same often applies to the stem and leaves of such Dicotyledons as form no secondary wood, though here exceptions occur even in relatively short-lived parts, as for example in the leafy stems of Thalictrum flavum and aquilegifolium. Tracheæ with bordered pits appear in the stem of most Dicotyledons and Gymnosperms which form secondary wood, at the point where the latter joins on to the primary bundles (cf. Chap. XIV), and occur further in the outer part of the bundle-trunks which traverse the leaf-stalks and leaves. The elements of this part are in many cases [1], especially among Coniferæ, very similar to those of the secondary wood in the stem generally, both in form and structure; yet this minute agreement is by no means of universal occurrence.

As the structure of the walls changes from within outwards, the width of the tracheæ increases in comparison with that of the primitive elements, and this change may take place according to the individual cases either gradually or suddenly, either constantly or so that narrower tracheæ again succeed the wider.

In very small bundles, containing only one or two tracheæ, the latter form a group which, though varying in individual cases, does not require a further description. On the other hand, larger bundle-trunks, which consist of numerous elements, show remarkable differences both in their arrangement and in their gradually changing width.

The collateral bundle-trunks of most Dicotyledons and Gymnosperms show the tracheæ ranged in rows running from within outwards, which touch each other laterally, or are separated by rows of non-equivalent elements. In every row the tracheæ become wider towards the outside, and in thick bundles soon attain an average size, which remains uniform in the whole region (Figs. 157, 158, 183). In the large bundles of many Dicotyledonous leaves the width of the elements first increases successively, and then diminishes again to an average size, which further towards the outside remains constant, e. g. leaves of Camellia, Ilex, Rosmarinus, species of Eucalyptus, &c. The difference between the narrowest and widest tracheæ is in all these cases moderate, especially in comparison with many Monocotyledons; the largest is 2–3 times as large as the smallest, or even less. The absolute size of the tracheæ is also moderate; in the leaves they are generally very narrow, falling far short of the average width of the tracheides and fibres of the secondary wood. Cf. the dimensions given in Sect. 40 and Chap. XIV.

In the thicker bundles of the Monocotyledons other conditions are the rule. In most cases the tracheæ here form two main rows as seen in cross-section, which diverge like the limbs of a V. At the point where the two limbs cut one another, or inside it, lie the primitive elements. The end of each limb is usually occupied by a

[1] Compare Frank, Botan. Zeitg. 1864, pp. 167, 393.

trachea, exceeding the primitive elements many times in width, with dense spiral, or narrow reticular thickenings on its wall; and this either forms the end of a continuous or interrupted row of successively wider tracheæ, or it follows suddenly on much narrower ones. In the middle between the two limbs there are either no vessels (even the whole Phloem may be included here, e. g. the leafy stem of Asparagus[1], and Tamus communis), or the middle is occupied and more or less filled up by a group of narrow, densely reticulated or pitted vessels, as for example in the Grasses (Fig. 151); and this group may spread out even beyond the external edge of the large tracheæ at the ends of the limbs (Fig. 147). In the laterally flattened Monocotyledonous bundles mentioned above, the tracheæ lie in an interrupted single, or in places multiple row, running from within outwards. In this it is usual for one or a few narrow primitive elements to be followed on the outside by one or a few tracheæ of considerable width, e. g. by a very large spiral tracheide in the leaf-stalk of Musa[2] and Canna, &c.; further outside there are either no more tracheæ, e. g. in the leaf of Pandanus[3], or some relatively very narrow ones, e. g. Musa, Canna, Heliconia, &c.: the broad bundles in the stem of many Palms, especially Calamus[4], though not laterally flattened, also show the same character; in Calamus some narrow spiral vessels are followed by a single pitted vessel of enormous width (cf. p. 169), and there are no others further outside.

The phenomena mentioned give rise to the characteristic habit of most Monocotyledonous bundles, which is especially evident in cross-section. They occur also among those members of the class which, like the Dioscoreæ, behave differently to the others with respect to the arrangement of the bundles (cf. p. 276). On the one hand, however, they are not confined to Monocotyledons, for the bundles in species of Ranunculus, and especially of Thalictrum, belong to or are closely connected with the form first described for Monocotyledons, while those of Nelumbium stand in the same relation to the second form. On the other hand, their distribution is by no means universal even in those families of Monocotyledons in which they prevail. The cross-section through the bundle-trunks in the leafy stem of Fritillaria imperialis and in the leaf of Phormium tenax[5] shows, for example, a triangular group (widening towards the outside) of moderately wide tracheæ, which increase but little in size towards the outside, and show the regular character and succession in the structure of their walls. The thicker bundle-trunks in the leaf of Yucca filamentosa (from which the thinner ones only differ in the number and size of their elements) show a thick xylem, broadly triangular in cross-section, in which the primitive elements are succeeded by a likewise broadly triangular group of spiral vessels with a closely-wound fibre, which are of moderate and tolerably uniform width. With this group is immediately connected on the outside a zone, consisting of about four cross-rows of narrower reticulated and pitted vessels, united at all points, which on the other side borders on the phloem.

The bundles of the Equiseta, to be further described below, agree essentially

[1] Von Mohl, *l. c.* Tab. G.
[2] Von Mohl, *l. c.* Tab. G, fig. 3.
[3] Von Meyen, Phytotomie, Taf. VIII.
[4] Von Mohl, *l. c.* Tab. D, F.
[5] Von Mohl, *l. c.* Tab. G.

in the arrangement of their tracheæ with the two-limbed bundles of Monocotyledons.

The arrangement of the parenchymatous cells of the xylem results for the most part from that stated in the case of the tracheæ. In bundles with many rows of tracheæ they form similar rows interpolated between the latter, with the form of narrow long medullary rays, round which, in a longitudinal direction, the lines of tracheæ run with slight undulations, alternately receding from one another and coming into contact at the ends of the rows of cells. In bundles of the Monocotyledonous type, with less regular seriate arrangement, they form single longitudinal rows, or groups of various form between the tracheæ. The cells themselves are elongated in different degrees, with horizontal or oblique ends, their walls delicate or considerably thickened and lignified; in the latter case their distinction from tracheides is often difficult.

(*b*) The *phloem* of collateral bundles consists of sieve-tubes, and thin-walled, elongated, prismatic cells, for which Nägeli's term *Cambiform*-cells is to be reserved. With reference to the more special structure three cases, not all equally well known, are to be distinguished.

1. In the more accurately investigated Monocotyledons (e. g. the Grasses, Fig. 150, with which the Equiseta appear also to agree), and no less in very many Dicotyledons, as Ranunculaceæ, Umbelliferæ (Fœniculum, &c.), Vitis, Aristolochia, also Cucurbita, &c., the cross-section of the phloem shows the two kinds of meshes, which have been known since Moldenhawer, and Mohl's Anatomy of Palms; some wider and polygonal, which are the cross-sections of the sieve-tubes, others narrower, square or rectangular, or frequently narrow and obliquely four-sided, representing the cross-sections of the cambiform-cells. The latter stand isolated among the sieve-tubes, distributed with varying regularity, so that as a rule each sieve-tube borders on another with one part of its lateral walls, and with another part on a cambiform-cell. Traced longitudinally the cambiform-cells form rows between the sieve-tubes, and parallel to them. Regarded individually they are as a rule shorter than, seldom as long as the joints of the sieve-tubes. Both from their arrangement in cross-section, and on tracing them in the longitudinal direction, it often has the appearance as if the cambiform-cells arose with the elements of the sieve-tubes from one mother-cell, the latter dividing longitudinally into a daughter-cell which becomes the sieve-tube element, and another which either becomes a cambiform-cell without further division, or is divided by cross-walls into several of them[1]. On this point, however, more accurate investigations must be undertaken[2]. The cambiform-cells have delicate non-lignified cell-walls and finely granular protoplasm, with a nucleus elongated in the longitudinal direction. On the structure of the sieve-tubes nothing need here be added to what was said in Chap. V.

2. In several, perhaps in numerous Dicotyledons (e. g. in the leaf-stalk of Olea Europæa (Fig. 156), in the stem of species of Lobelia, Crassulaceæ, Cacteæ[3]; and in several, especially succulent, Euphorbiæ, as E. Caput Medusæ), the cross-section of the phloem shows, among wider thin-walled elements, numerous or sparsely scattered groups of much narrower cells, each group often appearing from its size

[1] Compare Vöchting, Melastomeen, p. 16.

[2] [Compare Wilhelm, *l. c.* (see p. 172).]

[3] Compare Vöchting, Rhipsalideen, *l. c.* Tab. 52.

and arrangement as though it had proceeded from the longitudinal division of one of the wide elements. So far as investigations extend, the narrow elements are here sieve-tubes, which may be accompanied by narrow cambiform-cells; the wide ones are cells, whether they be called cambiform or simply parenchyma. More minute and extended investigations of these elements are wanting; they are usually curtly disposed of under the name cambiform or soft bast. In the thick bundles, often mentioned above, of Dicotyledonous leaf-stalks and ribs, the parenchymatous rows, resembling medullary rays, are continued directly outwards from the xylem into the phloem, and in the latter pass between bands of tissue, appearing irregularly narrow-meshed in cross-section, which no doubt contain the sieve-tubes.

3. In the primary bundles of the Coniferæ, especially of the leaves, where there is no disturbance from the secondary growth which quickly comes on in the stem, and also in the large bundles of the leaf of Welwitschia, the cross-section of the phloem shows regular rows of similar elements with soft membranes, which are in a very high degree capable of swelling. They are either present alone (Figs. 63, 157), or a single row consisting of relatively wide parenchymatous cells runs here and there between them, e. g. in the leaf of Dammara alba. The general form of the regularly serial elements first mentioned is elongated prismatic. How far they are sieve-tubes or cambiform-cells is undecided.

The development of the elements of the phloem of collateral bundles begins at the external edge and proceeds towards the xylem, and thus in the opposite order to that in the latter, i. e. centripetally in the phloem, if the centrifugal direction is maintained in the xylem. In the middle of the bundle, on the border between the two parts, active meristematic division may still be going on when the elements of the external and internal edge are completely differentiated.

The outermost, first-developed elements of the phloem (Russow's Protophloem) are often distinguished from those which follow by their smaller width, and thicker, apparently gelatinous walls; as regards their nature, however, they are in the cases now in question, which admit of more accurate investigation, partly sieve-tubes, partly cambiform-cells. In the thicker bundles they not uncommonly become compressed in the radial direction, owing to the expansion of the surrounding tissue, while their walls apparently swell up to the obliteration of their lamina—a phenomenon which ensues to a much greater extent in the old sieve-tubes and cambiform-cells of the secondary bast. (Cf. Chap. XV.)

The boundary between phloem and xylem is in most cases on the whole sharply marked, owing to the contrast between the delicate and non-lignified membranes on the one hand, and the characteristically thickened and lignified membranes on the other. The elements which form the boundary on the side of the phloem, no doubt always have the characteristics of cambiform-cells; it is not known that a sieve-tube ever borders directly on a trachea. In the thick bundles of the great majority of Dicotyledons the cells on this border-surface long remain capable of division, and when the differentiation of tissues has once begun at the periphery, their divisions take place chiefly in the tangential direction, parallel to the outer edge. Owing to the arrangement of the cells in radial or tangential rows thus determined in the zone indicated, the boundary is pretty sharply defined, even in cases where the actual divisions soon come to an end. In the stems of Dicotyledons and Gymnosperms

with secondary growth in thickness, this border-zone maintains its capacity for division, and becomes a portion, or a starting-point, of the cambial ring (Chap. XIV). In other bundles the cessation of the divisions takes place early in each transverse portion, simultaneously with the general differentiation of the tissues; and according to the degree in which this happens, the radially arranged boundary layer becomes less clear. It is therefore also, especially in Monocotyledons, the less possible everywhere to fix a sharp boundary between phloem and xylem, the less numerous and crowded the lignified elements in the latter are.

The word *Cambiform* used above was first adopted by Nägeli (Beitr. I. p. 4). For the meristematic strand giving rise to a vascular bundle, and consisting of thin-walled longitudinally extended cells in which longitudinal division goes on for some time, Nägeli uses the traditional and certainly ambiguous name Cambium, for which Sachs has recently substituted Procambium. The tissue of the phloem which has arisen from this cambium and passed over into the permanent condition is called by Nägeli in its totality the Cambiform, i. e. cambium-like tissue, as its elements are so similar to that of the cambium, in their elongated form and thinness of wall, that former observers have actually identified them with it. Our present knowledge imposes the necessity of severing the sieve-tubes from Nägeli's Cambiform, as a distinct kind of tissue. The name therefore, once being in existence, remains reserved for their characteristic companions, and may the better be used for them as it is for the most part literally applicable to them, even when the original meaning, indicated in Chap. XIV, and differing from that above-mentioned, is restored to the word cambium.

The structure of the phloem of collateral vascular bundles of the main stems has been described in the preceding paragraphs; the description was based primarily on the numerous investigations now existing of such objects as afford a clear and certain insight, owing to the size of the elements in question. It was already mentioned under 2 and 3, that in certain cases differences occur from the type described under 1, and that doubts exist as to the structure. Besides these definitely characterised cases, there are many others, especially concerning the smaller vascular bundles, in which we know nothing more of the structure of the phloem than that it consists of thin-walled, narrow, and elongated elements, the delicacy and smallness of which, as well as the tendency of their walls to swell, which interferes with their preparation, is deterrent to accurate research. Where these difficulties have already been successfully overcome, the structure described has always manifested itself. An uninterrupted series of transitions leads from the cases with relatively large, easily intelligible elements, to those where they are most delicate and difficult. No grounds whatever exist which would compel us to assume an essentially different structure. I therefore think that I am right in stating that the structure described exists in all vascular bundle-trunks here in question, and the more so as it is really not long since the largest sieve-tubes were first clearly recognised, as remarked at p. 182, and I do not doubt that further investigations, which are in any case a necessity, will justify what has been said.

In the xylem of many collateral bundles an intercellular passage occurs, which follows the course of the whole bundle, sometimes next to or within the otherwise persistent xylem, sometimes so that, though the latter is originally formed, the tracheæ become destroyed and degraded as the parts expand.

In numerous Monocotyledons, the Equiseta, and some Dicotyledonous water-plants, at the inner edge of the bundle, where the primitive tracheæ are placed, a passage is formed by the peripheral extension of the surrounding cells, i.e. schizogenetically (p. 200), while the external part of the xylem attains perfect development and is persistent. This severing of the original continuity of tissue goes on within the

wall of the primitive tracheæ; the latter are attached to the wall of the passage, and if its expansion is considerable they may be laterally removed from one another, and as the separation usually takes place before the elongation of the parts is complete, they become simultaneously distorted in the longitudinal direction, and reduced to thickening fibres adhering to the wall of the passage. This process often attacks annular tracheæ, the rings of which, in cases of great elongation, then become shifted to a long distance from one another. The width attained by the passage is various, sometimes equal to that of a moderate vessel, sometimes to the cross-section of the whole persistent part. The cells actively engaged in its formation undergo, on considerable expansion, divisions which are radial with reference to the passage, and remain as a rule thin-walled. These passages contain air, with the exception of some submerged plants to be mentioned below.

All collateral bundles of the stem of Equiseta show a relatively wide passage at the inner side of the xylem. The same phenomenon occurs very widely in the leafy stems (halms) and leaves of numerous Monocotyledons, but not in their rhizomes: thus in the stems of Hydrocharis, Butomus, Sagittaria, Alisma, Juncaceæ, Xyris, Cyperaceæ, Acorus Calamus, Leucojum, and Commelineæ (Tradescantia albiflora, zebrina, Lyonii[1]). As the names show, most but not all of these plants inhabit water or bogs. Further, the phenomenon does not occur in all the bundles of the same part; e. g. the smaller bundles in the leaf and scape of Acorus Calamus have no passage, while the larger bundles have a very wide one; and further, nearly related plants, agreeing in their mode of life (e. g. Grasses, Cyperaceæ, Commelineæ), often show a different character with reference to the width of the passage, and its presence or absence. Of Dicotyledons only some water-plants belong to this series, namely, the water Ranunculi and Nelumbium, besides those to be mentioned below. Both have a passage on the inner side of the larger, but not of the smaller vascular bundles of the stem.

In a number of water-plants the process described extends to the complete destruction of the whole xylem. The latter originates at an early age in the form of a few annular tracheides, or of a large number arranged in a bundle, all of which become both separated from one another laterally, and torn longitudinally, as the part elongates. The inconspicuous separate rings or fragments of rings remain adhering to the wall of the passage, the phloem, which is usually strongly developed, is alone persistent. As far as the investigations extend, these passages contain water. The leaf-trace bundles of the internodes of Potamogeton natans and its allies belong to this series;—in their cauline bundles and in the nodes the tracheæ are persistent—also the bundles of the leaf-stalk and flower-stalk of species of Nymphæa and Nuphar, and of Brasenia peltata[2]. In many bundles of the plant last-named a portion of the vessels are persistent; they thus belong to the former category; in their rhizomes no passages occur in the vascular bundles.—On allied phenomena in the non-collateral bundles of other water-plants, comp. Sect. 110.

A formation of passages in some degree different from that described occurs in the flower-stalks, leaf-stalks, and leaves of Aroideæ, especially of those with unisexual flowers, as Colocasia, Caladium, Richardia[3]. In the xylem only a few tracheides—

[1] Compare Frank, Beitr. *l. c.* p. 138.

[2] Compare Caspary, Berlin. Monatsberichte, 1862, *l. c.*—Trécul, Ann. Sci. Nat. 4 sér. tom. 1. p. 151.

[3] Duchartre, Recherches sur la Colocase, Ann. Sci. Nat. 4 sér. XII.—Unger, Beitr. z. Physiol.

2–4 in each cross-section — are formed, between delicate narrow cells; they are elongated, and ranged in longitudinal rows, one above the other, like vessels. One of these rows becomes expanded, according to van Tieghem's description apparently passively, to form a passage surrounded by narrow cells, the thickenings on its wall disappearing in places. The very oblique, fibrously thickened (unperforated?) end-surfaces, with which the articulations are in contact one with another, are persistent; in cross-sections, therefore, the passage often appears divided by a septum into two unequal portions. The other tracheides, lying partly inside, partly outside the dilated one, remain narrow and delicate, with annular or spiral fibrous thickening.

In the scape and leaf-stalk the passages increase in width with their distance from the periphery, the outermost bundles have only a narrow row of tracheides in place of them. They accompany the bundles into the lamina of the leaf, extending into the thick strand into which the bundles are united at its apex: here they lie close side by side in great numbers, forming the often-described water canals of the leaves of Aroideæ. In the leaves also they are accompanied by rows of tracheides which are not dilated, with which transverse anastomosing branchlets are everywhere connected, the petiole not excepted.

In the thicker bundles of the leaf of Sparganium ramosum a wide passage is produced, according to Frank[1], in the same manner as among the Aroideæ. The contents of the passages consist of air and watery liquid, while among the Aroideæ latex containing tannin is also present in places. Comp. p. 188.

The *sheaths* of collateral bundles consist either of simple parenchyma, or, rarely, of the form described as endodermis; or, lastly, and indeed in the majority of collateral bundle-trunks, of strands of sclerenchymatous or collenchymatous fibres, which accompany the bundles, whether it be as a tube encircling the whole bundle, or as a strand which partly surrounds the circumference of the bundle. In the latter case it rarely borders exclusively or principally on the xylem, but usually on the phloem, or only on its outer edge. These sheaths and accompanying strands are to be separated from the bundle itself, and considered in the following chapters. Here we have only to mention that those which consist of sclerenchymatous fibres may not uncommonly border immediately on the elements of the bundle, and even insert their own elements between the latter, so that the limitation, especially as seen in cross-sections, ceases to be clear, and the arrangement of the specific parts of the vascular bundle is often influenced in a peculiar manner.

A gradual transition from the sclerenchymatous elements of the sheath to the cells of the xylem very often takes place in cases where the latter are provided with strongly thickened and lignified membranes, e.g. in stout bundles of Monocotyledons. (Fig. 150.)

The sclerenchymatous sheath is generally very sharply limited on the side of the phloem; the latter lies as a uniformly thin-walled mass of tissue between the sheath and the xylem. It happens in rare cases that here also the sclerenchyma of the sheath penetrates deeply into the phloem, and is continued as far as the thick-walled

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d. Pfl. Wiener Acad. Sitzgsber. Bd. XXVIII. p. 111.—De la Rue, Botan. Zeitg. 1866, p. 816.—Van Tieghem, Struct. des Aroidées, *l. c.*

[1] Beitr. p. 137.

cells of the xylem. In the stem of Rhapis flabelliformis most bundles have a phloem which is somewhat crescent-shaped in cross-section; it is surrounded by a thick sheath forming a bundle of fibres, which projects strongly towards the outside; round the small xylem, consisting of a few vessels surrounded by thick-walled cells, the sheath is feebly or not at all developed. In some of the inner bundles a ridge-like projection about three layers thick passes from the sheath to the thick-walled cells of the xylem through the middle of the phloem, severing the latter into two symmetrical halves. Essentially the same phenomenon appears much more conspicuously in the stem of Calamus. The xylem, as already stated at p. 323, always shows some narrow spiral vessels, and outside these a very large pitted vessel; around and between them lie thick-walled elongated cells. In the smaller peripheral bundles the single phloem, semicircular in cross-section, lies on the outside of the pitted vessel, and is surrounded by a strong sheath of fibres, which is continued round the xylem. In most bundles the phloem is divided by a broad continuation of the sheath, extending up to the pitted vessel, into two portions lying right and left of the latter. Each of these portions consists of some large sieve-tubes (comp. p. 176) standing in a row parallel to the circumference of the vessel, together with the accompanying cambiform cells. This row also may once more be interrupted by sclerenchyma, so that individual sieve-tubes with their accompanying cells stand isolated in the sclerenchyma of the sheath[1].

In the mature leaf of species of Pandanus, the phloem appears at the first glance to be wholly absent even in thick bundles, and in its place a strong narrow strand of sclerenchymatous fibres seems to border immediately on the xylem[2]. More accurate investigation shows isolated sieve-tubes between the sclerenchymatous fibres. In younger bundles they are easier to find—perhaps also more numerous; it seems as if here, as in other bundles, sieve-tubes present at an early period were afterwards crushed by the neighbouring cells and rendered unrecognisable, but this has still to be investigated.

As the parts belonging to and bordering on the vascular bundle must in fact be considered in connection with one another, it seems more expedient here, in conclusion, to collect together some figures referring to collateral bundles, explaining them with reference to the paragraphs above, than to insert them among the preceding descriptions of the individual parts.

Fig. 149. Cross-section through a mature internode of Equisetum

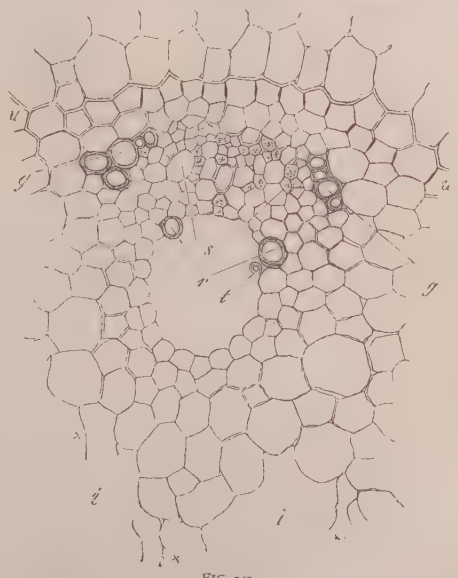

FIG. 149.

[1] [Compare Kny, Verhandl. d. Bot. Ver. Prov. Brandenburg. Bd. XXIII, 1881, pp. 94–109; also his Bot. Wandtafeln, V.]

[2] Compare Meyen, *l. c.* (p. 323).—Van Tieghem, Ann. Sci. Nat. 5 sér. VI. p. 197.

palustre (145). *u* Endodermis. *i* axial air-canal, at *x* remains of the membranes of shrivelled pith-cells. In the middle a vascular bundle surrounded by parenchyma, without a distinct sheath. At the inner edge of the bundle lies a wide intercellular passage, in which the letters *r*, *t*, *s* are written. *t* an annular fragment, adhering to the wall, of the membrane of a primitive tracheide for the most part destroyed. *r* persistent annular tracheides. *g* groups of the last developed, likewise permanent, annular and reticulated tracheides, distinguished from the surrounding tissue by the shading of their walls. *s* the phloem; in this the wider lumina belong to the sieve-tubes (cp. p. 180), the narrower ones, some of which are granularly dotted, to the cambiform-cells. The double-contoured bands on the outer edge of the phloem, inside the layer of cells following *u*, indicate the collapsed primitive elements of the phloem (Protophloem).

Figs. 150 and 151 represent two cross-sections through a bundle of the leaf-trace of Zea Mais, at different parts of its course. Fig. 150 (550), from Sachs's Text-book, is from

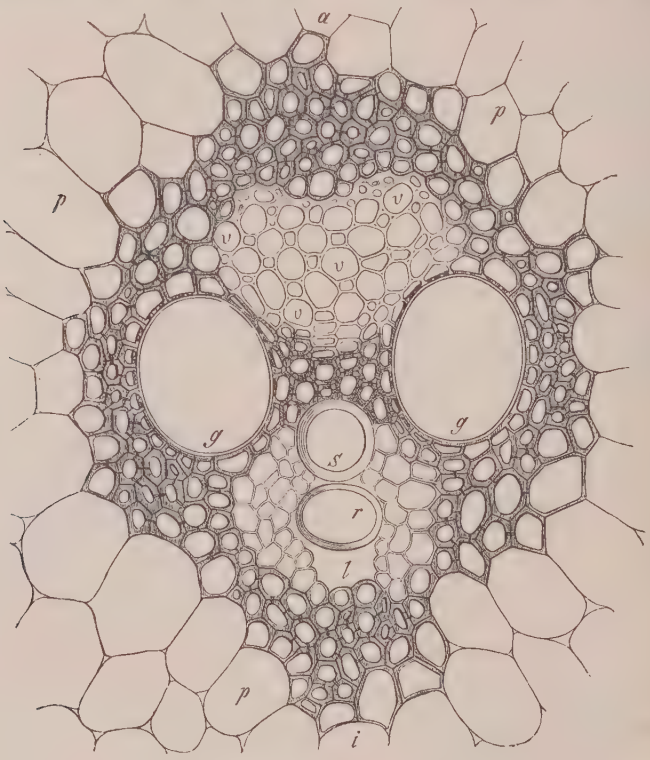

FIG. 150.

the stem. *g*–*g*, *s*, *r*, *l*, the xylem, *v* the phloem. In the latter *v*, *v* indicate the sieve-tubes, between which the narrower cambiform cells stand in regular distribution. At the outer edge of the phloem are its narrower, thick-walled primitive elements. On the inner edge of the xylem in an intercellular passage, *l*, bounded on the outside by the ring, *r*, of a primitive annular vessel, partly destroyed by the longitudinal extension. *s* spiral vessel. *g*, *g* large vessels with (unbordered) pits, or narrowly reticulated. Between the phloem and *s*, *g* and *g* a transverse group of narrow pitted vessels. A sheath composed of sclerotic lignified elements goes all round the bundle; *p*, *p* thin-walled parenchyma outside the sheath. *a* outer edge, *i* inner edge of the whole bundle. In the lamina of

the leaf and the upper part of the leaf-sheath the bundles are similar to that in Fig. 150, though on the average smaller.

Fig. 151 (145), on the other hand, is taken from the place where the bundle passes through the basal portion of the leaf-sheath of a young plant. The bundle itself, with its group of vessels at *g*, is in all parts smaller than that in the preceding figure, but otherwise similar to it, as is clear without explanation, even in the finer points of structure not represented in the figure. Here however there is a single-layered sheath, consisting of delicate parenchymatous cells, square in cross-section, around the whole bundle. Outside this, and separated by it from the phloem, is the thick strand of collenchyma, *sc*. Both the latter and the bundle are surrounded by the parenchymatous layer *st*, which is rich in starch (the starch-sheath, Sect. 122). *e–e* Epidermis of the outer surface.

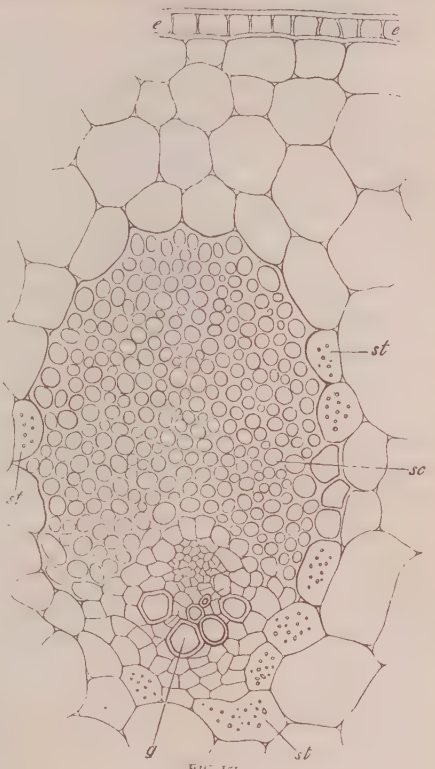

FIG. 151.

Fig. 152. Cross-section through a vascular bundle of the internode of a creeping stem (runner) of Ranunculus repens (225). *xx* annular and spiral vessels at the inner edge. *t* pitted vessels in the external region of the xylem; between and around the latter delicate-walled elongated parenchymatous cells. *s* phloem; the larger meshes are sieve-tubes, the smaller ones, partly dotted, are cambiform cells. At the inner border of the phloem are delicate cambiform cells in rows. Externally to its constantly thin-walled peripheral elements, the bundle is surrounded by a thick sclerenchymatous sheath, which is only interrupted on the outer border of the xylem. Outside this is large-celled, thin-walled parenchyma. The longitudinal section through the bundle, if not quite accurately median, would be similar to that of Saururus, represented in Fig. 57, p. 157.

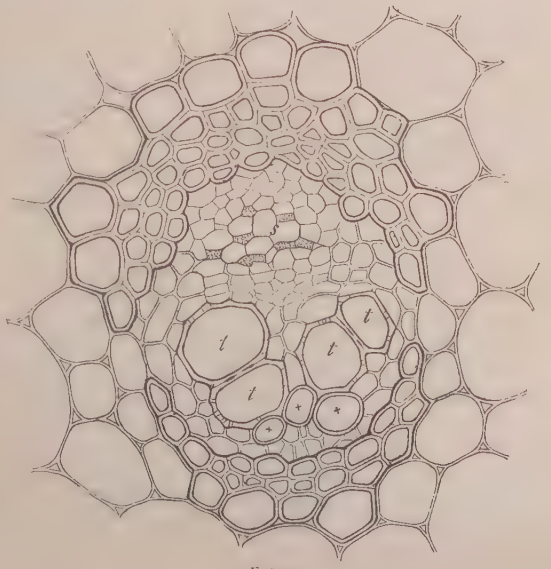

FIG. 152.

Fig. 153 (225) represents the cross-section of one of the larger bundles in the internode of Ranunculus

fluitans. The structure is similar to that of the preceding species, but simpler. $g\times$ trachea with annular and loosely spiral fibres, bordering on an intercellular passage in which the letter is written. g wider tracheæ with densely spiral and reticulated wall. s five relatively large sieve-tubes between narrow cambiform cells. The whole bundle is surrounded by narrow elongated prismatic cells, showing non-lignified cellulose walls, and these pass over gradually on the outside into large-celled parenchyma with abundant starch. As regards the surrounding layer marked u it remained doubtful whether it has an indication of endodermal structure on those walls which are radial with reference to the bundle.

Figs. 154 and 155, from the fully elongated hypocotyledonary stem of Ricinus communis (from Sachs' Textbook), represent that form of bundle, with radially disposed xylem, which predominates among Dicotyledons, together with the initial stages of the secondary growth in thickness, which here follows immediately on the formation of the primary bundles. In the cross-section (Fig. 154) g, t, t are the rows of vessels alternating with rows of thick-walled cells, beginning at the inner edge of the bundle with the primitive elements, which are distinguished by the thick shaded walls. t narrower, g wider pitted vessels. y phloem consisting of sieve-tubes, cambiform and delicate parenchyma, with three bundles of sclerenchymatous fibres on its outer border, at b. On the boundary between xylem and phloem, the formation of the zone of cambium and secondary growth (c–c) has begun by means of tangential divisions, and is continued, starting from the sides of the vascular bundle, over the parenchymatous zone cb, cb: cf. Chap. XIV. m parenchyma of the

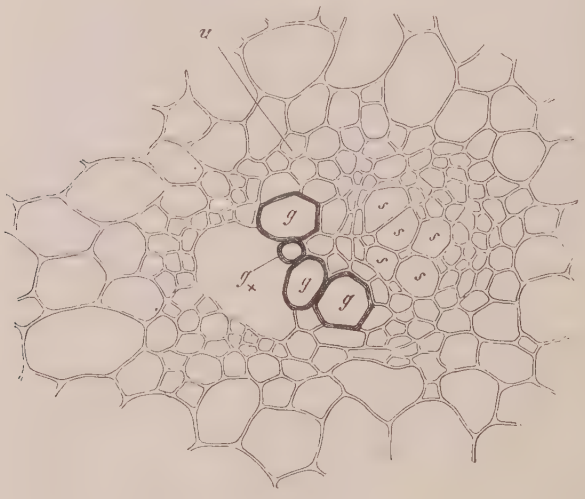

FIG. 153.

pith, r of the outer cortex. Between the layers containing the letters b and r is the parenchymatous sheath containing starch-grains (Starch-ring, Chap. IX). Fig. 155 is the radial longitudinal section through a bundle of the same structure as Fig. 154. The letters r, b, c, m indicate the same things as in the former figure. p bands of parenchyma from the phloem. s innermost and narrowest spiral vessel. s' a wider one. l scalariform reticulated vessel. t mature vessel with bordered pits; at q the perforated transverse wall between two elements. t' a pitted vessel still immature, the borders of the pits not yet developed. b, b' thick-walled cells of the xylem; on the wall of t and t' the boundaries of cells which have been cut through are visible. b'', b''' narrow tracheides (?).

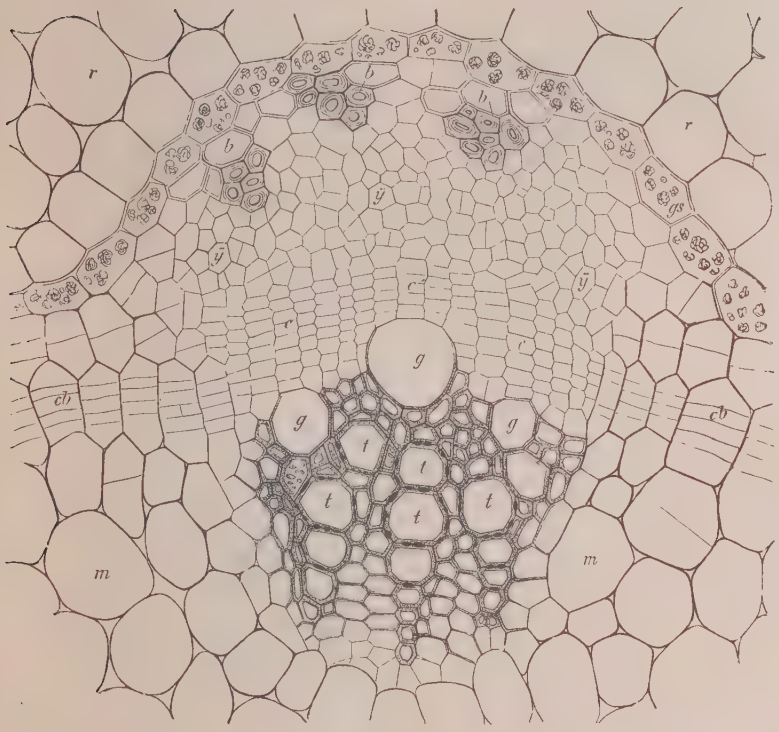

FIG. 154.

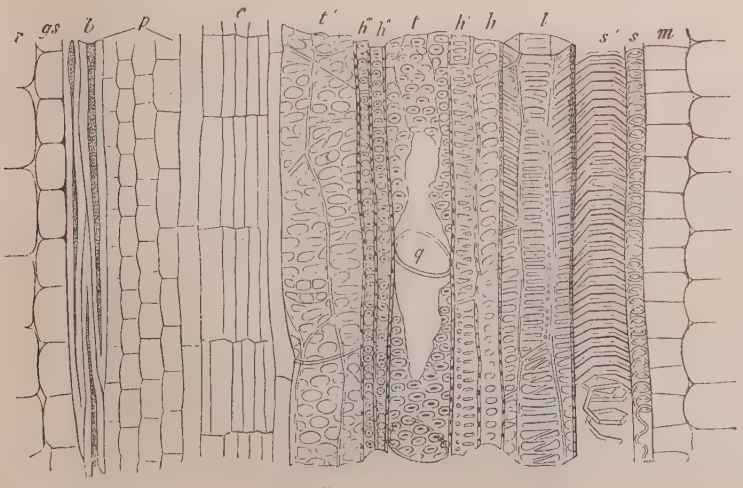

FIG. 155.

Fig. 156. Cross-section through the vascular bundle in the midrib of the leaf of Olea Europæa (375). *s–s* the phloem, consisting of wide (parenchymatous?) cells, and scattered groups of very narrow elements (sieve-tubes?); comp. p. 325. *f–f* sclerenchymatous fibres, forming a girdle round the outer edge of the phloem, and occurring scattered on the inside of the xylem. The very dense xylem borders on the phloem internally; the primitive elements at its inner edge do not appear clearly; its larger external portion consists of radial rows of thick-walled pitted tracheæ, which alternate with bands of parenchyma. The latter are indicated by the granular dotting of the lumen. *p* parenchyma.

FIG. 156.

Fig. 157. Cross-section through a vascular bundle in the leaf of Welwitschia mirabilis (145). An uninterrupted zone of very thick-walled and elongated sclerenchymatous fibres surrounds at *f* the outer edge of the phloem, and at *f'* the inner edge of the xylem. Inside the zone *f* follows the phloem, which is crescent-shaped in cross-section, consisting of narrow, radially arranged, elongated elements; their structure could not be detected with certainty, nor are they drawn quite accurately in the figure, because the great swelling of the membranes makes it impossible to spread out the cross-section of the phloem in one plane, in such a preparation as that figured. The inner portion of the xylem enclosed by the fibrous sheath *f'* consists of tolerably wide, elongated prismatic cells, connected without intercellular spaces, with thick almost gelatinously soft membranes. Between them are inserted numerous, very narrow, compressed and distorted, spiral and annular tracheides, with thick, distorted, fibrous thickenings; *sp*; they doubtless represent the primitive elements of the bundle. Further outside follow the persistent tracheæ, placed in tolerably regular rows, here and there alternating with delicate cells, and in general increasing in width in each row from within outwards; first annular and spiral tracheæ, with dense and very broad thickening layers, then reticulated and (at *g*) large pitted vessels, with bordered pits and round perforations in the cross-walls. *t, t* are the rows of pitted and reticulated tracheæ in cross-section; they surround the bundle

and are to be described below in Sect. 112. They also occur on the right-hand side of the figure, and may be known by their notched outline. *p* parenchyma of the mesophyll, with an indication of the small crystals of Calcium oxalate imbedded in the walls.

Sect. 102. The bundles of the leaves of Cycadeæ and Isoetes, with which perhaps those of Phylloglossum agree, are different from the typical, simply collateral bundles in the arrangement and development of their parts.

Fig. 157.

The peculiarity of these bundles, expressed generally, consists in the fact that the essential elements of the xylem are reversed in position and order of development, as compared with those in the typical cases. In the plants first named there are the additional peculiarities that tracheides appear at a later stage on the border of the phloem, and that the bundles are in many cases united in pairs.

The bundles of the leaf-trace of the Cycadeæ begin in the stem, according to Mettenius[1], as simple collateral bundles, and run out in the same form into the sheathing bases of the leaves, but before entering the petiole of the foliage-leaves, or the apex of

[1] Abhandl. d. K. Sächs. Gesellsch. d. Wissensch. VII. p. 573.

the scale-leaves, they assume a changed structure, which they maintain throughout their whole course in the leaf. In the round cross-section of the bundle (Figs. 158, 159), a small group of narrow spiral tracheides (*sp*) (the primitive elements of the xylem) occupies about the centre. From this an uninterrupted group of large prismatic pitted tracheides (the inner portion of the xylem) extends towards the inside; this group occupies the entire inner side of the bundle, and has in cross-section the form of a

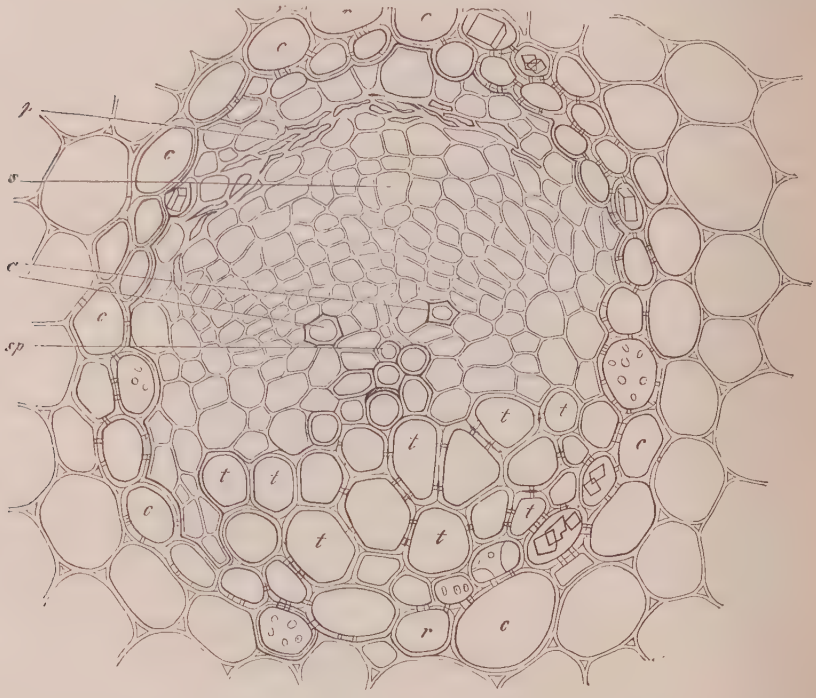

FIG. 158.—Cycas revoluta. Petiole of a small foliage-leaf belonging to a young plant; vascular bundle, cross-section (225). Explanation in the text. The spiral tracheide *sp* is connected with the inner pitted tracheides *t* by means of a group of annular and reticulated tracheides. In *c* here and there fragments of the large crystals of Calcium oxalate.

sector of a circle with the centre at the primitive tracheides. The remaining part of the bundle, lying outside that described, is principally formed of thin-walled elements, ranged in radial rows: next the outer edge are several concentric rows of sieve-tubes (*s*), separated by delicate parenchyma; the outermost row which bounds the bundle, being in the mature condition compressed in the manner often described, and thicker-walled than the rest, bordering the outer edge as a narrow shining band (*p*); on the boundary of the xylem, so far as present investigations extend, only prismatic cells occur, without sieve-tubes. To these parts is finally added an *external* portion of the xylem, developed in centrifugal order, outside the primitive tracheides; this forms a small group of pitted tracheides (*a*) ranged in irregular radial rows, which are separated from one another, from the primitive tracheides, and from the inner portion of the xylem, by thin-walled elements. As the bundles become thinner in

their course through the leaf, the thickness of the individual portions diminishes, especially the external portion of the xylem. In many species, at any rate, the bundles in the cross-section of the leaf-stalk are generally arranged in the figure of an inverted Ω, with the limbs directed towards the upper side. In the constricted part of the figure either they are separate, the constriction being open; or they approach one another in pairs, the inner vascular portions of each pair being turned towards one another, and the scalariform vessels of each in uninterrupted connection over a broad surface. In Zamia longifolia one such coupled bundle is present near the middle of the cross-section; in Dion there are about six of them forming a row vertical to the surface of the leaf[1]. Other species of Zamia show, according to Mettenius, a less regular grouping of the bundles and of their connections.

In Cycas revoluta the bundle is encircled by a thick-walled sclerotic sheath,

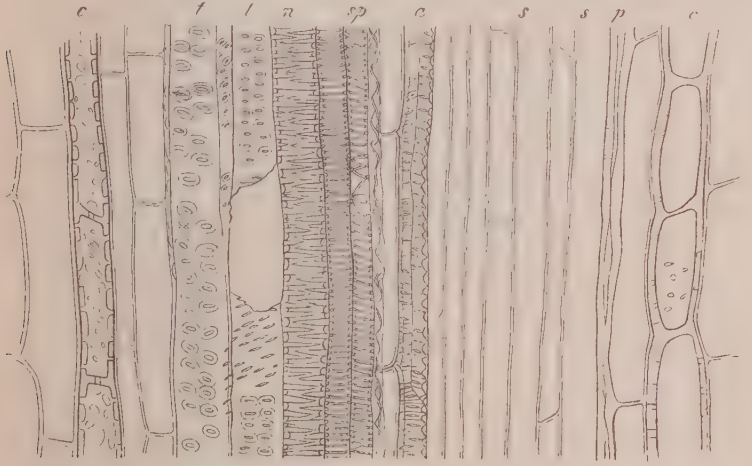

FIG. 159.—Cycas revoluta (225). Longitudinal section through a similar bundle of the same leaf-stalk, in the direction r—r, Fig. 158. The letters have the same meaning as in that figure. *n* reticulated tracheide with narrow slits; the fibres of the narrowest (first) spiral tracheide are distorted.

sharply limited both inside and out, which consists of short, wide, angular elements (*c c*), with pitted or narrowly reticulated walls, and cavities often filled up by large crystals of Calcium oxalate. In the other species investigated, there is no sheath which can be sharply distinguished from the surrounding parenchyma; at most some of the sclerenchymatous fibres, which are scattered through the whole tissue, stand around the periphery of the bundle.

According to Russow[2], the feeble leaf-bundles of Isoetes closely approach those of the Cycadeæ as regards structure. They are collateral and their orientation is normal. Their xylem consists of narrow prismatic parenchymatous cells, with some narrow, spiral, and reticulated tracheides standing between them. The primitive elements appear, according to Russow, on the boundary of the phloem, while the others, which are nearer the inner edge of the bundle, attain their development later. On the inside of the phloem thin-walled prismatic elements can be distinguished, but

[1] Mettenius, *l. c.* p. 573, Taf. 1, fig. 10.

[2] *l. c.* pp. 140, 155.

no evident sieve-tubes; on its outer border are thick-walled cells, which latter in the terrestrial species assume the characteristics of tough fibrous cells. On the border of the phloem and xylem there lies in most species in the middle of the bundle a single intercellular canal, while in I. Engelmanni there are usually three of them; their origin is not clear[1]. The radial walls of the layer of cells bordering these canals have in I. Engelmanni (Russow) and I. Durieui the characteristics of the radial walls of the endodermis. No such structure is present at the periphery of the bundle.

In connection with Isoetes, Phylloglossum may be mentioned, as the short description by Mettenius[2] shows at least this one point of agreement, that its vascular bundles only contain a few delicate tracheides, with annular thickenings, or spiral fibres which can be unwound. The phloem is at any rate very inconspicuous; according to Mettenius it is even in many cases wholly absent.

Sect. 103. The form of collateral bundles above designated as the *double* or *bicollateral* is distinguished from the simple collateral form by having two groups of phloem, one being situated as in the latter on the outside of the xylem, and a second on its inner side. In all other respects they agree with the simple form[3].

As the type of this form of bundle are to be mentioned in the first instance all leaf-trace bundles of the Cucurbitaceæ, and in fact of all species investigated[4]. Both groups of phloem have the typical structure described (p. 324, 1), and are especially remarkable for the size of their sieve-tubes (chap. V). They are frequently connected by means of a narrow band, fringing the lateral edge of the bundle, and containing some sieve-tubes, so that in these cases the bundle, strictly speaking, belongs to the concentric type. The xylem is constructed altogether on the collateral type; on the inside are narrow annular and spiral vessels; towards the outside are reticulated vessels becoming gradually wider, and finally very large pitted vessels with short articulations. The latter are surrounded by broad layers of cells, some of which are elongated, with thick pitted walls, while others are short elements with undulated surfaces fitting into one another, and round-meshed reticular thickenings on their walls. It remains to be investigated whether, or how far these elements should be called tracheides.

A bicollateral structure is presented by the leaf-trace bundles of many Dicotyledons, which belong to the ring: Melastomaceæ[5], Cichoriaceæ, Solanaceæ, Asclepiadeæ, and Apocyneæ; Strychnos, and Daphne. In many of these the inner phloem is so widely separated from the rest of the bundle, that it may be regarded as a distinct strand of sieve-tubes; in other cases distinct strands of sieve-tubes occur side by side with the inner groups of phloem of bicollateral bundles, e.g. Cichoriaceæ, Solanum tuberosum, and dulcamara; comp. p. 231. Of the Myrtaceæ already mentioned at p. 231, Eucalyptus globulus decidedly belongs to this series. All the investigated species of Eucalyptus, Metrosideros, Callistemon, Melaleuca, and Myrtus, have on the inner side of the primary bundles a group of tissue consisting of delicate narrow elements, and, according to what has been found in the case of Eucalyptus globulus, it is very probable that these groups have the same nature as those in the latter

[1] Compare A. Braun, Isoetes-Arten d. Insel Sardinien, Monatsbericht. d. Berlin. Acad. 1863.

[2] Botan. Zeitg. 1867, p. 99.

[3] [Petersen, Ueber das Auftreten bicollateraler Gefässbündel in verschiedenen Pflanzenfamilien. Engler, Bot. Jahrb. 1882, p. 359.]

[4] Compare Dippel, Mikroskop, p. 225; Bryonia.

[5] Vöchting, *l.c.*

plant. No accurate investigations of them however lie before us, and the example of Welwitschia (p. 335) shows that one must be cautious in coming to a decision on apparently bicollateral bundles. On the behaviour of Trapa, which here remains to be mentioned, comp. sect. 105.

2. *Concentric Bundles.*

Sect. 104. In concentric bundles one of the two parts occupies the middle, and is encircled by the other.

Of the two cases here possible, the one, namely that in which the phloem occupies the middle and is surrounded by the xylem, occurs in the lower ends of the leaf-trace bundles of many, but not of all rhizomes of Monocotyledons, where they lie at the periphery of the bundle-cylinder in the stem, e. g. Iris germanica, Cyperus aureus, Papyrus[1], Carex arenaria[2] (but not, for example, C. disticha and C. hirta), Acorus Calamus and A. gramineus[3]. This form arises no doubt from the collateral bundle, as in its course the xylem gradually surrounds the phloem more and more on both sides, until the latter is completely enclosed; where it does occur however this form must be distinguished from the typically collateral. The structure and the surrounding tissues present no generally valid differences from collateral bundles. The phloem, which is round as seen in cross-section, is as a rule surrounded by a single, or rarely by a multiple ring of reticulated or pitted vessels, with parenchymatous cells interspersed between them. Comp. fig. 148, p. 317.

Sect. 105. The other possible case, that the xylem occupies the middle and is surrounded on its whole surface by the phloem, occurs in individual Dicotyledons with anomalous distribution of the bundles, also in isolated cases among the Cycadeæ, and is characteristic of the entire group of Ferns, with a few exceptions, partly mentioned above.

Among Dicotyledons the medullary and cortical bundles of the Melastomaceæ[4] may first be mentioned. In these the centre is occupied by a few narrow vessels, which are scattered among delicate prismatic cells, the vascular group being surrounded by a delicate ring, consisting of sieve-tubes and cambiform cells. In feeble bundles only one single, narrow, spiral vessel often occurs, and even this may be absent, so that we then have the sieve-tube bundles mentioned at p. 231.

According to Reinke's description, all the bundles of the stem of the species of Gunnera, especially G. scabra, also belong to this series; so also do those in the stem of Auriculas (cf. p. 251). In the leaf of the plants last-named the bundles are collateral, and are arranged in a row as usual among Dicotyledons. The collateral structure also holds good for the smaller bundles of the stem, even when almost circular in cross-section; on the one side is a small group of narrow, primitive, spiral tracheæ, with larger reticulated vessels external to them; on the other side is the small phloem, the whole being surrounded by delicate cells, bounded externally by the endodermis. On the other hand, the larger bundles of the stem of Pr. auricula show a concentric arrangement; the narrow primitive elements are in the middle,

[1] Link, Icones Anatomicæ, Tab. V. figs. 1, 9; IX. fig. 6.
[2] Treviranus, Physiol. I. p. 195, Taf. III. [3] Van Tieghem, *l. c.*
[4] Sanio, Botan. Zeitg. 1865 p. 179.—Vöchting, Melastomeen, *l. c.*

surrounded successively by the wider vessels, the phloem, and the endodermis. It is manifest that this structure may come about owing to the frequent junctions of the smaller collateral bundles.

The above-mentioned isolated occurrence of concentric arrangement in the Cycadeæ was found by me in some of the small bundles in the petiole of Dion; they had a round xylem, surrounded by a phloem with its elements in radial rows.

Lastly, the axial bundle (described at p. 277) in the internodes of several Dicotyledonous water-plants must be placed here: namely, Hippuris, Trapa (?), Callitriche, Bulliarda, Elatine[1], Hottonia, and Myriophyllum. It consists in general of a central xylem, completely surrounded by a phloem, both parts usually having abundant delicate parenchyma between the essential elements. In the cases of Hippuris, Trapa, Hottonia, and Elatine Alsinastrum, the persistent vessels are arranged in an interrupted ring, which surrounds a relatively thick cylinder of parenchyma ('pith'). The phloem is bounded on the outside by an endodermis. In the leaves of these plants, with the exception perhaps of Callitriche, the bundles are collateral, with normal orientation. The axial bundle of Verhuellia (p. 278) also seems to belong to this series, though Schmitz could only detect that it consists 'of a strand of prosenchymatous cells, in the middle of which runs a single spiral-vessel.' All the cases here cited, with the exception of the three elucidated by Sanio, Vöchting, and Hegelmaier, require still more accurate investigation.

In *Bulliarda aquatica*, according to Caspary's description, the middle of the stem is occupied by a thin cylindrical strand consisting chiefly of elongated cells, in which, about midway between periphery and centre, lie two indistinctly separated groups of annular and spiral vessels, which run out to the leaves. In *Elatine Alsinastrum* the axial cylindrical strand consists permanently, as regards its main bulk, of much elongated cells; a few cell-layers inside its periphery, one vessel for each leaf of the whorl next above it first appears, and in the node this vessel bends out into the leaf at right angles; or, to express the fact differently, the vascular elements running into the leaf here abut on the cauline vessels. The vessel itself appears to be the continuation of the one which has passed out at the next lower node. Later on other isolated wider vessels are formed side by side with the original ones; in cross-section all are arranged in an irregular ring. Sieve-tubes lie in the zone outside the vessels. Axial vessels are not present at the beginning; after those of the leaf-trace however 1–2 vessels appear and are permanent. *Hottonia* appears (judging from very incomplete investigation) to behave similarly, apart from the obvious differences due to difference of Phyllotaxis, and with the further distinction that axial vessels do not occur.

The often investigated axial bundle in the stem of *Hippuris*[2] shows in its early stages, as first accurately described by Sanio, annular and spiral tracheæ at its centre, which are scattered among thin-walled prismatic cells, and are cauline, with acropetal growth. At a later stage vessels are formed at the periphery of the cylinder, and from these the bundles branch off, which pass transversely through the cortex into the leaves. They are connected with one another in the node, and in the cross-section of the internode they represent an irregular, many-layered and often-interrupted ring, in which the vessels increase in width in the centrifugal direction, according to their order of origin. Outside the vascular ring lies a many-layered ring of prismatic cells, and between the

[1] [F. Müller, Struktur einiger Arten von Elatine; Flora, 1877.]

[2] Von Mohl, Verm. Schr.; Palm. Structura, Tab. g, fig. 2.—Nägeli, Beitr. *l.c.* p. 56.—Sanio, Botan. Zeitg. 1865, p. 191.

latter are small bundles of sieve-tube, each consisting of one, or rarely two sieve-tubes[1] surrounded by a layer of cambiform-cells.—Both vessels and sieve-tubes run vertically and separately in the internode. In the node the equivalent elements anastomose with each other, and the two kinds of elements unite to form the vascular bundle, and enter the leaf. The peripheral elements of the axial strand which we have described are persistent. The cauline axial tracheal elements begin to disappear on the first appearance of the peripheral vessels, and become so crushed by the surrounding prismatic cells that a mature bundle encloses a dense parenchymatous 'pith' within the peripheral vascular ring.

One bundle runs out into each of the leaves, which form multifoliate whorls, and usually each has a separate course from the rest; yet it not uncommonly happens that a common trunk arises from the vascular cylinder of the stem, and then, towards the periphery of the stem, divides into two or even three leaf-strands.

In the stem of *Callitriche*[2] the thin axial bundle, consisting chiefly of delicate elongated prismatic cells, contains at its apex an axial annular or spiral vessel, which grows acropetally, and projects far above the last node which contains vessels; close by this a second (and a third) soon appear. The first two primordial vessels have a position in the internode corresponding to the two opposite leaves of the adjoining node; in the node a small bundle branches off from them for each leaf. As the internodes become elongated 2–12 wider annular or reticulated vessels appear, by the side of and somewhat external to the primordial elements; they are arranged in two irregular groups, and are persistent, while the primordial vessels soon disappear in the internode, and are replaced by an axial intercellular passage, to the wall of which their remnants adhere. This passage may subsequently be filled up again by the luxuriant growth of the neighbouring cells. In the node the axial passage between the vascular elements, which are here densely crowded, is absent. The vascular group is surrounded by a small zone of phloem, consisting of a few rows of narrow elements, and bounded on the outside by the endodermis.

In *Trapa* the wide central portion of the axial strand consists, in the fully elongated internode, of loose, large-celled parenchyma, traversed by numerous longitudinal air-passages; a relatively narrow, peripheral, annular zone consists of thin-walled prismatic cells. Among the latter are large vessels arranged in a circle at wide intervals. Their primitive elements appear to run out into the leaves, but to be distorted and indistinct, each being in many cases replaced by an air-passage when the internode has attained its definitive elongation. The large persistent annular vessels are apparently of later origin. Outside and inside the vascular circle Sanio[3] found a circle of scattered sieve-tube-bundles, each of these consisting of one sieve-tube with horizontal cross-walls, surrounded by a layer of cambiform tissue.

Myriophyllum spicatum[4] has in the young internode, when elongation begins, in the middle of the axial cylinder a central group consisting first of one and then of 2–4 spiral vessels, which are in close contact with each other. This group is cauline and grows acropetally, and in the node branches grow out from it centrifugally into the leaves, which are ranged in alternating, usually quadrifoliate whorls. In the leaf the vessels are united with a small phloem to form a collateral bundle. From the node the four phloem-bundles of the whorl—which require further histological investigation—run down, as a

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[1] The sieve-tube nature of these elements is disputed by Russow, who however includes them in his protophloem.

[2] Nägeli, *l.c.*—Hegelmaier, Monogr. d. Gattg. Callitriche.—Idem in Martius, Flora Brasiliensis, fasc. 67.

[3] Botan. Zeitg. 1865, p. 193.

[4] Vöchting, Zur Histologie und Entwickelungsgesch. v. Myriophyllum, Nova Acta Leop. XXXVI. 1872.

leaf-trace, radially and tangentially vertical, in the periphery of the axial cylinder. Each passes through two internodes, and at the third node, above one of the leaf-bundles which pass out here, splits into two short, strongly-diverging limbs, each of which attaches itself to the nearest of the bundles coming down from the second node.—The main mass of the axial cylinder consists permanently of thin-walled prismatic cells. When elongation is complete, the axial bundle of spiral vessels disappears, while round its circumference larger thick, and usually reticulated, vessels appear, which are scattered and arranged in irregular rings. Also the number of the supposed sieve-tubes at the periphery increases with age, so that the original arrangement may become indistinct.

Sect. 106. The vascular bundles in the stem and leaves of the Ferns[1] belonging to the divisions Polypodiaceæ, Cyatheaceæ, Hymenophyllaceæ, Gleicheniaceæ, Schizæaceæ[2], and Marattiaceæ, to which the Selaginellæ are to be added, are of various size and form; in cross-section they may be circular, elliptically trapezoidal, band-shaped or plate-like; the outline of the broad ones being even, wavy, folded in a furrow-like manner, or with the edges bent in; others are annular or tubular (e. g. stem of Marsiliaceæ, Microlepia, Dennstædtia, &c., see p. 284), or forming peculiar symmetrical figures resembling an *X*, *V*, *U*, Ω, &c.: the bundles of the leaves may be similar to those of the stem to which they belong, or very different from them. Comp. Figs. 128–141. Their structure is as uniform as it is distinct from that of most other forms of bundle. Comp. Figs. 160, 161.

The middle is occupied by the xylem, the form of which is either identical with that of the entire bundle, or similar to it, or in various degrees different; the former for example is the case in the annular or band-shaped bundles, and also in the approximately cylindrical ones of the stem; while the latter condition occurs especially in leaf-stalks, in such a manner that the symmetrical figures mentioned are peculiar to or especially marked in the xylem, the outline of the whole being simpler. The former may even be severed into two symmetrical groups in one bundle, as for example in the leaf-stalk of Aspidium molle, Polypodium phymatodes.

The xylem consists, as regards its main mass, of wide, long, prismatic to spindle-shaped, scalariform tracheides with bordered pits (comp. p. 165), and only in rare cases of scalariform vessels, with septa perforated in a scalariform manner (Pteris aquilina, p. 162). Between, or more rarely on the outside of these, lie, at definite points, some narrow spiral and narrow scalariform tracheides, which are the primitive elements at the origin of the xylem; from these the development of the wide tracheides starts, and advances centrifugally with reference to each point of departure, though, it may be, centripetally with reference to the whole bundle. The position and number of these primitive groups are different in the individual cases. In bundles presenting an angular or unilaterally elongated cross-section, one such group lies at or near each corner, or at each end of the greater diameter of the section, as in the flat bundles in the stem of most Selaginellas (comp. Fig. 131, p. 282),

[1] Von Mohl, Structura filic. arborearum, *l. c.*—Link, Icones selectæ, Heft. III. und IV.—Mettenius, Angiopteris, *l. c.*—Karsten, Vegetationsorgane der Palmen, *l. c.* pp. 117, 130, &c.—Dippel, Verhandl. der Naturforscher-Versammlung zu Giessen (compare p. 180), and Mikroskop, p. 198 ff.—Trécul, Sur la position des Trachées dans les Fougères, &c.; Ann. Sci. Nat 5 sér. tom. X. p. 344, tom. XII. p. 219 ff.—Russow, Vergl. Untersuchungen.—With reference to the form of the bundles, compare also Presl and Reichardt in the works cited at p. 298.

[2] [See Prantl, Unters. z. Morph. d. Gefässkrypt, Heft. II. Leipzig, 1881.]

where they lie in the corners themselves, and are continued into the leaf-bundles, which join on here (comp. p. 282); and in the band-shaped or symmetrically many-rayed bundles of the leaf-stalk of Ferns[1]. In bundles which are elliptical in cross-section, e.g. in the rhizome of Pteris aquilina, their position corresponds approximately to the foci of the ellipse. Besides these primitive groups occupying the ends and corners, others may be present in the same xylem, e.g. in the band-shaped, symmetrically curved bundles from leaf-stalks, represented by Russow; a median group occurs in Gleichenia vulcanica, Aneimia Phyllitidis, Marsilia Drummondii; in Asplenium Filix-femina there is a median group and an intermediate one in each side between this and those at the margin; in Balantium Culcita there are two intermediate groups, and so on. In roundish or circular and in annular xylems several primitive groups are scattered about the cross-section; five for example in the annular

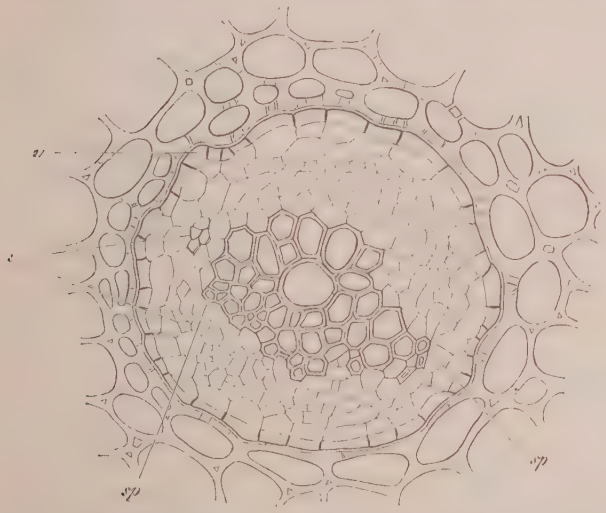

FIG. 160.—Polypodium vulgare; rhizome; cross-section through a weak vascular bundle (225). *s* phloem region, sieve-tube structure not clear; *sp* narrow spiral tracheides of the xylem, the wider elements which constitute the majority are scalariform tracheides; *u* endodermis apparently derived by tangential division from the same layer of mother-cells with the parenchymatous layer adjoining it on the inside. Outside *u* is parenchyma. The pitting on its cell-walls is essentially the same everywhere; in the figure it has only been indicated at certain points. Those of its cells which border on *u* are thicker-walled on the inside than elsewhere.

bundles of the stem of Marsilia Drummondii; six, according to Russow's description, in the vascular cylinder of Trichomanes radicans, three near the middle in the round axial bundle in the small stem of Selaginella spinulosa. In very small bundles there is often only a single primitive group present, which is more or less eccentrically placed, e.g. small bundles in the rhizome of Pteris aquilina, Angiopteris (Mettenius, *l.c.* 517). In the large flat bundles in the stem of Cyatheaceæ the primitive groups have only recently been discovered by Trécul. Here they occur in the form of narrow reticulated tracheides at the edges bordering the leaf-gap, enclosed among the scalariform tracheides, or in a narrow notch between them; and from here they proceed, or send branches into the bundles of the leaf-stalk. In consequence of early

[1] Cf. Russow, *l.c.* Taf. X; especially abundant details in Trécul, *l.c.*

compression and distortion they are only to be detected in the mature stem with great difficulty, and often there are only traces of them.

The xylem is either composed of tracheides only, without any non-equivalent elements interposed between them, or there are groups and rows of parenchymatous cells containing small starch grains, intermixed with them[1]. The two conditions are distributed according to species and perhaps genera, not according to the form of the bundle. The first, for example, occurs in Marsilia and Pilularia, where the xylem is an uninterrupted, one to three-layered ring of tracheides; also in the axial bundles of the Selaginellas, and in many flat, round, and angular bundles of Polypodiaceæ, e.g. in the stems of Polypodium vulgare (Fig. 160), P. Lingua, Davallia pyxidata; the petioles of Asplenium auritum, Scolopendrium vulgare, and many others (cf. Russow, *l.c.*) In the bundles of the Marattiaceæ also, no parenchymatous cells, or extremely few of them, occur among the tracheides.

The other case occurs, for example, in the relatively thick cylindrical xylem of the rhizomes of Trichomanes radicans, Gleichenia, and Lygodium, in the annular bundle in the rhizomes of Microlepia and Dennstædtia, in the round or flat bundles of the stems of Pteris aquilina (Fig. 161), Polypodium fraxinifolium, Platycerium alcicorne, Alsophila microphylla, Cyathea Imrayana, and arborea; in the bundles of the leaf-stalks of Trichomanes, Aspidium Filix mas, molle, Lygodium and many others (comp. Russow, *l.c.*). The axial bundle in the stem of the Schizæas is also placed in this category by Russow, and no doubt rightly, for although a many-rowed uninterrupted ring of tracheides appears to surround a thick axial pith-cylinder of parenchyma, yet it is not separated from the latter in the manner to be described below, which is characteristic of all other bundles of Ferns belonging here, but the two are in immediate contact, so that the strand in question must naturally be regarded as a xylem with a coherent axial cylinder of parenchyma. In the leaf-stalk of Trichomanes pinnatum and elegans[2], and in that of species of Aneimia, Gleichenia and Schizæa, very thick-walled, lignified, sclerenchymatous fibrous cells are added to the tracheæ; there is a thick bundle of them in each corner of the V which the xylem

FIG. 161.—Pteris aquilina. A quarter of the cross-section through a large vascular bundle of the stem; cf. Fig. 143, p. 295. *S* spiral tracheids, *g*—*g* wide scalariform vessels (cf. p. 162), *sp* sieve-tubes, *b* the protophloem of Russow, *sg* endodermis, *p* the parenchyma surrounding it, containing starch-grains; *K* thickened portions of the wall of the vessels between the rows of scalariform pits. Between *b* and *sg*, and in the xylem, especially round *S*, are thin-walled parenchymatous cells, containing starch. From Sachs' Textbook.

[1] Russow's 'companion cells' (Geleitzellen).

[2] Mettenius, Die Hymenophyllaceen, p. 421.

forms in Trichomanes, and of the approximate T which it forms in Schizæa pectinata; in Gleichenia dichotoma and polypodioides they lie isolated and often separated from the tracheides by parenchymatous cells along the edges of the V-shaped xylem.

The xylem is surrounded in all cases, in annular bundles both within and without, by a many-layered complexus of tissue, which is to be regarded as the phloem, Fig. 161. One or a few layers of parenchymatous cells, containing starch, and similar to those of the xylem, border immediately on the latter. Outside the parenchymatous layer comes an annular zone, which contains the sieve-tubes, though in the smaller bundles, as already mentioned at p. 181, the latter are certainly not always to be clearly distinguished. When distinctly developed they form a usually single, but in some places double annular ring, and are in contact with each other by means of those walls which are radial with reference to the centre of the bundle. This zone is then followed all round on the outside by a likewise annular zone of elongated fibre-like elements with narrow lumina, characterised by thick, brilliant, and soft walls. These are called by Dippel bast-fibres, and by Russow protophloem, because they appear as the primitive elements of the phloem, and here also it remains doubtful whether they are to be reckoned among the sieve-tubes, or regarded as special organs. They are partly in immediate contact with the indubitable sieve-tubes, and even frequently inserted in the same circle, while in other cases they are separated from them by small parenchymatous cells. Finally, a one or few-layered sheath of parenchymatous cells containing starch, which are often tolerably wide, and always differ from those outside the bundle in their form and their (smaller) size, completely surrounds the zone of sieve-tubes and fibres, and, apart from a few exceptional cases to be mentioned below, this is in its turn enclosed by a single-layered endodermis, which limits the bundle sharply on the outside. This consists of prismatic, usually inconspicuous cells greatly flattened from without inwards, with a moderately thick, usually brownish membrane, which soon becomes cuticularised, and which in the radial walls is easily torn across, so that in sections the whole endodermal sheath is often split, and difficult to recognise. In especially favourable cases (e. g. species of Polypodium) every cell of the endodermis stands exactly in front of a cell of the parenchymatous layer adjoining it on the inside, so that the common origin of the two from one layer of mother-cells is recognised at once. Even where the latter is not the case, the origin of the two is the same, at least among the true Filices and Marsiliaceæ[1].

Among the plants belonging to this series the Marattiaceæ and Selaginellæ are destitute of an endodermis[2]. The bundles of the former appear simply inserted in the parenchyma, and this applies both to the petiole and to the stem. So at least I found it in young stems of Angiopteris, and I can only suppose that the figure cited by Russow from De Vriese and Harting's Monogr. des Marattiacées (Taf. VII. Fig. 3, 4), according to which the case would be different in the stem of Angiopteris, represents the section of a root passing through the stem, for in the root the endodermis is always present[3]. In the Selaginellæ the phloem is surrounded by a dense layer of small-celled parenchyma.

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[1] Russow, *l. c.* p. 195.

[2] [Compare Treub, Recherches sur les Organes de la Vég. du Selaginella Martensii, Leide, 1877.]

[3] Compare Sachs, Textbook, 2nd Eng. ed. p. 420, supplementary remarks.

In petioles, when the xylem is concave or notched, strands of cells 3–4 rows thick, which are distinguished from the rest of the parenchyma by their very wide lumen, are to be found in its depressions and furrows, sometimes just in front of the primitive tracheides; 'in longitudinal sections they are conspicuous from the fact that their walls are irregularly bent in and out, and are connected with those of the neighbouring cells in such a manner that large cavities or intercellular spaces arise; in old bundles it is usually found that the walls have become brown.' Russow calls them cavity-parenchyma (Lückenparenchym). The tracheides bordering on them usually have very irregularly developed spiral bands. Examples: species of Asplenium, Cyathea microlepis (Dippel), *l. c.*, Aspl. Filix femina, Cyatheaceæ[1], e. g. Cyathea medullaris. The wide cells in Osmunda regalis to be mentioned below may also belong here.

From its general distribution among the Fern group in the widest sense, one may term the structure of the bundle just described the Fern-type. At the same time different degrees of deviation from the type occur within this group. Those described in the Marattiaceæ and Selaginellæ are trifling. The Lycopodiaceæ, of which we shall treat in the next section, are closely connected with the Selaginellæ in the structure of the bundle, as well as in other points. In this respect the Equiseta are most widely different from the Fern-type; their strictly collateral bundles, which most closely resemble those of Monocotyledons, were described above (p. 329). Besides these, the Ophioglosseæ, and in part at least the Osmundaceæ, have collateral bundles. The two parts have normal orientation in the round or flat bundles, the xylem is similar to that of Ferns, with some narrow spiral tracheides (primitive elements) at its inner edge; its main bulk consists of large prismatic tracheides, which in Ophioglossum (pedunculosum and vulgatum) show narrowly scalariform reticulate thickening without pit-borders, while in Botrychium they have very thick reticulate fibres, with elliptical bordered pits in the meshes of the reticulations. Parenchyma is present in the xylem of the annular bundle in the stem of Botrychium rutæfolium, in the form of radial bands resembling medullary rays; I could not find any in the examples of B. Lunaria, which I investigated. The phloem appears very similar to that of the typical form; the wide elements presumed to be sieve-tubes still require more exact investigation (p. 180). The bundles of the petiole, and the small bundles of the stem of Ophioglossum, which in cross-section are arranged in a circle, are not bounded externally by any kind of distinct sheath. The bundle of the stem of Botrychium Lunaria and rutæfolium, which is annular in cross-section, is encircled on the outside by an endodermis, the cells of which do not differ from those of the surrounding parenchyma, except in the exquisite undulating longitudinal bands in the middle of their radial side-walls.

In Osmunda (compare p. 280) the bundles of the stem are collateral. The xylem, where it enters the circle of bundles, is horseshoe-like in cross-section, and during its descending course becomes narrowed to a wedge-like form; internally it borders directly on the parenchyma of the pith; it has the same structure as in the typical Ferns, and has hardly any parenchyma inserted among the scalariform tracheides. The groups of xylem are separated from one another in the whole longitudinal

[1] Russow, *l. c.*

course of the bundles, by medullary rays 6–10 cell-layers in breadth. Round this ring of separate groups of xylem runs a common annular phloem-region, which is similarly constructed to that of the typical Fern-bundle: outside each group of xylem are first some layers of small-celled parenchyma, then an almost uninterrupted zone of large sieve-tubes running round the whole stem; this zone is usually one layer thick outside the xylem-groups, while in front of the medullary rays it is many-layered, and projects into them like a wedge. The layer of sieve-tubes is next immediately bounded on the outside by a layer of transversely elongated, partly thick-walled elements, which in their turn are separated from the brown sclerotic tissue of the stem by a many-layered zone of parenchyma. Outside the transversely elongated zone runs an endodermis, which in the mature condition can be recognised by the brittleness of its radial walls. In the petiole of Osmunda the funnel-shaped xylem is surrounded by a similarly-formed zone resembling the phloem of typical Fern-bundles, which in the mature state is bounded on the outside by a very indistinct endodermis; this zone however, as also stated by Dippel, only contains sieve-tubes in its broader convex half. On the concave side it is parenchymatous, and distinguished in cross-section by 10–12 small groups of conspicuously wide cells, which still need investigation[1]. In the stem of Todea Africana and T. hymenophylloides the structure of the vascular bundle is like that described for Osmunda, only the form of the xylem is in some degree different in consequence of the fusions of laterally adjoining bundles. In the lowest part of the leaf-bundle, which has the same shape as in Osmunda, sieve-tubes are, in T. Africana at least, present on the concave side as well. In the leaf-stalk of T. Africana I found the endodermis scarcely recognisable, while in T. hymenophylloides it is very clear.

The axial strand, which the collateral bundles in the stem of Isoetes unite to form, consists of a roundly angular mass of short and irregularly spindle-shaped, reticulated and spiral tracheides, and of thin-walled parenchymatous cells irregularly distributed between them, these elements together forming the xylem. The latter is completely surrounded by a transparent mantle of shortly-prismatic or tabular cells, with contents clear like water, and a strongly refractive membrane, which is provided with broad and very delicate pits, but no clear sieve-pores. Russow is no doubt right in considering this mantle as a peculiarly imperfect phloem of the axial strand, especially as the equivalent parts of the leaf-bundles pass over into it directly. With reference to its phenomena of growth it will have to be further spoken of in Chap. XVIII.

This may probably be the most fitting place to mention the axial bundle, which traverses longitudinally the leafless stolons of Nephrolepis tuberosa, N. acuminata, and N. exaltata[2]. In the structure, form, and centripetal development of its xylem this agrees completely with the 5–6 rayed radial bundles in the roots of Ferns to be described below. Here also, as in the latter, phloem-groups alternate with these rays, and appear to contain relatively wide sieve-tubes, but I am doubtful whether the narrow primitive elements of the phloem do not also completely surround the rays of the xylem. At any rate the whole inner part of the bundle is surrounded by about two layers of very narrow elements, and the latter usually by two layers of wider parenchymatous cells, on which

[1] Compare Dippel, Russow, *l. c.*

[2] Trécul, *l. c.*—Russow, *l. c.* p. 100.

the endodermis borders externally. The xylem consists in the middle of wide scalariform tracheides, and interstitial bands of Parenchyma. According to all the data, which however require to be more exactly established, the bundles described may represent an intermediate form between the concentric and radial Fern-bundles. According to Russow the likewise axial bundle of the stolons of N. pectinata and rufescens has not the structure described.

3. *Radial Bundles.*

Sect. 107. The radial bundles are closely connected with the concentric by means of those in the stem of Lycopodium, and by the diarch forms, which occur in many roots. In the typical cases they are distinguished by the fact that in the radial bundle the xylem forms several bands running out radially from the centre, between which lie the same number of groups or bands of phloem alternating with them. In all radial bundles the development of the characteristic elements, both of the xylem and phloem bands, begins at the periphery, and proceeds thence with varying celerity towards the middle. The primitive elements, which in the xylem are here also distinguished by their narrowness, form the peripheral ends of the rays. As these thus form the points of departure of the development of xylem, it is usual to speak of the number not of the rays, but of the starting-points—of di- to polyarch bundles[1].

Radial bundles occur in the stems of Lycopodiaceæ, and in the filiform stolons of Nephrolepis; and in all roots, with a few exceptions mentioned at p. 319.

The axial strand which traverses the middle of the stem of Lycopodiaceæ agrees, with the exception of its radial structure, with the bundles above described in the stem of the Selaginellæ (with the exception of S. spinulosa), which, in the structure and development of their xylem, correspond to the diarch or oligarch radial forms.

In the stem of *Psilotum*[2] this strand is cauline, not receiving or giving off leaf-strands. In the branches which appear above ground the cross-section of the whole is almost circular, bounded on the outside by an endodermis, which only differs from the surrounding parenchyma in its undulating radial walls. The xylem is triarch to pentarch and octarch; its not always equidistant rays are separated from the endodermis by one or a few layers of relatively narrow, elongated, prismatic parenchymatous cells, and consist at their peripheral ends of a group of narrower reticulated tracheides (I did not find spiral tracheides), and towards the centre of a few rows of scalariform tracheides; these rows do not reach to the middle of the bundle, but abut on a strand of elongated prismatic, pointed sclerenchymatous fibres, which traverse the middle. The rest of the substance of the bundle consists of thin-walled prismatic parenchyma, in which, especially at its periphery, are scattered some few-celled groups of somewhat narrower and thicker-walled sieve-tubes. This designation is at least justified by the appearance of the smooth lateral walls, agreeing with that in the Ferns, by the granular contents adhering obstinately to the walls, and by the absence of nuclei, which is very conspicuous on comparing these elements with the surrounding cells; on the thin oblique terminal-surfaces of the articulations I believe that I have directly

[1] Nägeli, Beitr. *l. c.* p. 10.

[2] Nägeli, *l. c.*—Russow, *l. c.* p. 131.

seen delicate sieve-pores. In the subterranean shoots of the rhizome (Nägeli and Leitgeb's rhizoides) the bundle is very weak and rudimentary in its development; I find only a flat or three-cornered xylem, consisting of a few, frequently only 3–6, reticulated and scalariform tracheides, separated here and there by thin-walled elements; the peripheral tracheides are but little narrower than the internal ones; the xylem is completely surrounded by 2–4 layers of delicate spindle-shaped cells. I could see nothing of any sieve-tubes. The vascular bundle of Tmesipteris appears from Russow's statement to have a similar structure to that of Psilotum.

In the cylindrical axial strand of the stems of *Lycopodium* (comp. p. 281) the xylem consists of a number of plates or bands, the peripheral corners of which are each formed by a group of narrow tracheides (comp. p. 163), the above-described points of attachment of the leaf-trace bundles, while the larger inner part consists of wider scalariform tracheides. (Comp. Fig. 162.) The number and arrangement of the plates and their relations to the rows of leaves vary with the species, and with the vigour of the individual shoots. Of the latter relations we have already spoken above. As regards the other conditions which come under consideration[1], among the native species investigated L. inundatum has 3–5 plates, united in the middle to form a body which has a stellate cross-section, thus constituting a tri- to pentarch radial xylem. The latter is however even here not unfrequently in so far irregular, that one or the other plate separates from the rest, so as to have an isolated course for some distance, and then again to unite with the others. Four radial plates united in the middle are present in the ultimate ramifications of the heterophyllous species, as L. complanatum, and as a rule L. alpinum, though here deviations occur in 20–30 per cent. of the cases. In the stouter axes of the last-named species, as well as in L. clavatum, annotinum, and Selago, the number of the vascular plates is higher, being in proportion to the thickness of the shoots; in stout main stems of L. complanatum and alpinum, for example, it amounts to 11 and 13, in those of L. annotinum and clavatum to 17, but diminishes again in the weaker ramifications to 4 and 3. In these cases the plates are only partially, or scarcely at all radially convergent; most of them rather form separate bands in the decidedly bilateral prostrate main-shoots of all species possessing them (Fig. 162), these bands being slightly curved, with their convex surface always directed towards the lower side of the stem, and their corners lying chiefly right and left; they are further united with each other in a great variety of ways, sometimes radially, sometimes so as to form loops. Their union and

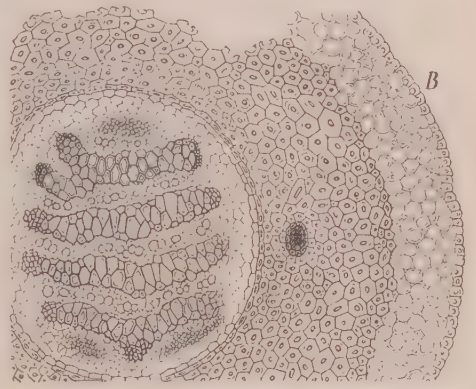

FIG. 162.—Lycopodium Chamaecyparissus. Cross-section of a shoot, magnified about 100 times. In the middle the cylindrical vascular strand; in the dense cortex to the right the cross-section of a bundle running into a leaf. From Sachs' Textbook.

[1] Hegelmaier, *l. c.* p. 790.

separation vary in successive sections of their longitudinal course. Feeble branches of higher order once more show a more radial arrangement and mode of union. In the non-bilateral stems of L. Selago radial union of all the 4–6 plates is, according to Hegelmaier, the more frequent case, while irregular winding and grouping are more rare. For further details compare the treatises cited at p. 281. The intermediate spaces between the vascular plates, which are usually smaller than the latter, are occupied by the one or more masses of phloem of the bundle, each constituting a correspondingly-shaped group of elongated prismatic parenchymatous cells with oblique ends, and apparently oily contents, among which lies a usually simple interrupted row of wider sieve-tubes, represented by the wider, somewhat more strongly contoured meshes of Fig. 162 (comp. p. 181).

The walls of all the elements of the phloem are soft, swell strongly in water, and become blue with solution of iodine in potassium iodide. Between the peripheral angles of the vascular plates, and alternating with them, lies in each phloem-portion a small group of thick-walled, narrow, elongated fibrous elements,—the primitive elements of the phloem. Round all the corners runs a zone of prismatic parenchyma, usually two cell-layers thick, of the same or similar cell-form and structure to that of the phloem, but in most species (L. clavatum, annotinum) distinguished by intercellular spaces, and loose, easily separable connection of the cells. A sheath, consisting on the average of two layers of tangentially elongated cells, possessing thin walls, cuticularised according to Russow, and not undulating, surrounds the whole vascular bundle, and unites it with the inner cortex, which according to the species is parenchymatous or sclerenchymatous.

The stout roots of Lycopodium clavatum[1], Alpinum, and species of similar growth, have essentially the same structure as the stems. In the two species mentioned the xylem is hexarch to dekarch, very often heptarch, and then so arranged in the simplest most regular case as to form three separate plates, one being diametral, while two stand symmetrically in front of the two surfaces of the first; these two are concave, with U-shaped cross-section, and with the concavity turned towards the periphery. Every plate diminishes in breadth in the centripetal direction, and often consists in the middle of only a single scalariform tracheide. Irregularities and interruptions of the plates occur similar to those in the stem. In the heptarch or octarch examples of L. clavatum investigated, I almost always found one of the concave plates larger, and of narrow horseshoe-like cross-section, the other smaller and much flatter, with a separate, in cross-section elliptical or wedge-shaped, vascular strand (in itself monarch), lying in front of its slightly concave outer surface. Other arrangements however occur, and these are sometimes most irregular and involved. The structure of the surrounding tissue and of the spaces between the vascular plates is the same as in the stem. In the branches of these roots the number and arrangement of the plates become reduced and simplified as the thickness diminishes; their last ramifications—and in L. Selago and inundatum all roots of every order of ramification—have only a vascular group surrounded by a phloem, which is perhaps only parenchymatous (?). In the branches of the root of the stouter species first-named, the

[1] Nägeli und Leitgeb, Entstehung, &c. der Wurzeln, p. 117, &c.—Van Tieghem, Ann. Sci. Nat. 5 sér. tom. XIII.

former consists of a few small vessels lying on one side of the cylindrical bundle. In the roots of L. Selago and inundatum a strongly-curved, diarch vascular plate, sickle-shaped in cross-section, lies, according to Russow's description, inside the cylindrical phloem, the sieve-tubes being situated between its limbs.

Sect. 108. In the great majority of roots the axial bundle which traverses them is of very regular radial structure, which in its principal characters is uniform in all cases[1].

The approximately cylindrical bundle is surrounded by an endodermis, which is either permanently undulated, or is only so at first, becoming sclerotic in the mature condition. According to its origin the endodermis is not to be assigned to the bundle, but forms the innermost (limiting) layer of the surrounding cortex. The xylem is according to the particular case diarch or polyarch, and its starting-points, corresponding to what are afterwards its peripheral corners, all lie at equal distances from one another: in diarch bundles at diametrically opposite points of the circular cross-section; in all other cases removed from each other by the fraction of the periphery determined by their number ($\frac{1}{3}$, $\frac{1}{4}$, &c.). From the starting-points vascular plates develope in a radial direction, and in centripetal order of development; and these either meet in the centre or do not reach it, but remain separated by a parenchymatous or sclerenchymatous mass, which permanently occupies the middle of the bundle. The same number of phloem-groups alternate with the vascular plates, to which they thus correspond in number and arrangement.

The xylem and phloem-rays are separated from each other by delicate parenchymatous cells, and in fact two layers of the latter may as a rule be distinguished between each xylem and the next phloem group; more rarely only a single layer is present, or there are more than two. On the outside an uninterrupted zone of parenchyma, which usually forms a single layer, more rarely two layers, and rarely several, constitutes the limit of the whole bundle towards the endodermis. In the case of the Ferns, Nägeli and Leitgeb have called this limiting layer the *Pericambium*, a name which it may here bear generally, even where, as in Equisetum, its origin is different from that in the cases for which it was first introduced. In Monocotyledons however cases are not rare, where the outermost vessels border directly on the endodermis, and the Pericambium is thus interrupted at every xylem-plate, and only surrounds the phloem-rays.

Van Tieghem calls the whole of the cells, which are interposed between the groups of xylem and phloem, and thus unite them into a dense cylinder, conjunctive tissue (tissu conjonctif). The latter forms, as has been said, the usually two-layered bands between the xylem-plates and phloem-groups, and is continued inwards between the former in cases where they do not meet. Externally it borders on the pericambium. The latter is called by Van Tieghem in the case of the Phanerogams the rhizogenic layer, from the function which it performs in the origination of lateral roots.

[1] Nägeli, Beiträge, *l. c.* p. 23.—P. van Tieghem, Recherches sur la symmétrie de structure dans les Plantes vasculaires. I. La racine. Ann. Sci. Nat. 5 sér. tom. XIII.—Nägeli und Leitgeb, Entstehung d. Wurzeln, München, 1867.—Nicolai, *l. c.* (compare p. 231).—See also Link, Icones anatomicæ.—Schacht, Lehrbuch, p. 167, etc.

For the structure of the individual parts few general rules are to be given, except those which hold good generally for vascular bundles and their sheaths. The xylem-plates consist of one or more rows, which, according to the particular case, are uninterrupted in the radial direction, i. e. one trachea follows on another; or they are interrupted by the interposition of non-equivalent (parenchymatous or sclerenchymatous) elements. For the special nature of the tracheæ, i. e. whether they are vessels in the strict sense or tracheides, the rules and difficulties stated at p. 164 apply. The first-formed vessels or tracheides, which occupy the corners, are always narrow, the later ones, following in a centripetal direction, become suddenly or successively wider. The latter are always pitted or reticulated vessels (or tracheides); the narrow peripheral ones are as a rule also reticulated or annular vessels, with dense and fine thickening fibres, the prevalent direction of which is transverse. For short distances however the fibre has not uncommonly in these cases also a simply spiral course. Closely wound spiral fibres, which can be unrolled for a long distance, occur more rarely, e. g. in the roots of Tornelia fragrans, Cucurbitaceæ, Anthriscus Cerefolium (Van Tieghem), Phaseolus (Dodel), Cycadeæ (Mettenius), and Coniferæ.

The structure of the phloem-rays, where they are well developed, is essentially the same as in the typical collateral or concentric bundles. In feeble roots of Monocotyledons they are not uncommonly reduced to one sieve-tube with narrow-celled surrounding tissue (e. g. Triglochin maritimum, Aponogeton, Hydrocleis Humboldtii, Potamogeton lucens, comp. Van Tieghem, *l. c.* Taf. VI), this being of typical structure, only small. It is therefore to be supposed that the typical structure belongs to them generally, though they still require more exact investigation, especially in the small-celled bundles of Dicotyledons. I should also wish to extend the last remark to the roots of Coniferæ, in the primary bundles of which, according to Janczewski's more recent statement[1], sieve tubes are said to be wholly wanting.

The number, and with it also the arrangement and relative breadth of the xylem and phloem-rays, the extent and distribution of the tissue occurring around and between them, lastly the special structure of the particular forms of tissue, and thus the entire structure of the root-bundle, vary, sometimes in different roots of the same species, sometimes according to the species and the larger systematic divisions. In the former relation the general rule holds good that as the thickness of the roots diminishes, not only does the number of the tissue-elements in the bundle diminish, but also the number of its radial plates, if in the thicker specimens this exceeds two. Further slight individual differences, which cannot be referred to difference in thickness, occur among members of the same species. In the other relation, besides the obvious identity or similarity of structure of closely related forms with similar adaptation, the great conformity of structural plan in all divisions of vascular plants is to be emphasised. For none of them can a special structure be stated as everywhere characteristic of the group. Van Tieghem's first plate shows the almost identical cross-sections of young roots of Cyathea medullaris, Allium Cepa (main root of the seedling), Taxus, and Beta. Smaller differences between subdivisions of the larger classes are often more sharply expressed. The existing investigations give rise to the following rules:—

[1] Ann. Sci. Nat. 5 sér. tom. XX. p. 31.

1. In almost all *Dicotyledons* where the point has been investigated, the original bundle of the root is oligarch, usually with 2, 3, or 4 rays, more rarely with 6 or 8, while higher numbers occur exceptionally. In the *main-roots* the xylem-plate is usually diarch-diametral, triarch, or tetrarch; higher numbers occur rarely, whether in single individuals (as 5–7 in specimens of Vicia Faba, and perhaps even 12[1], instead of 4), or as the rule for certain species, as most Amentaceæ (*Quercus* sp. 6–8, Alnus 5–6, Castanea 6–12, Fagus 8, Carpinus 4), Æsculus (6), Coffea (8), &c. None of these numbers are constant absolutely and without exception even for the particular species. Whether a definite number can be characteristic of one of the larger genera or of a natural family (apart from occasional individual variations) is not to be decided from the existing data. At any rate this is the case in several families of which a dozen or half-a-dozen representatives have been investigated. Diarch xylem-plates occur, for example, in the main root of all investigated Cruciferæ

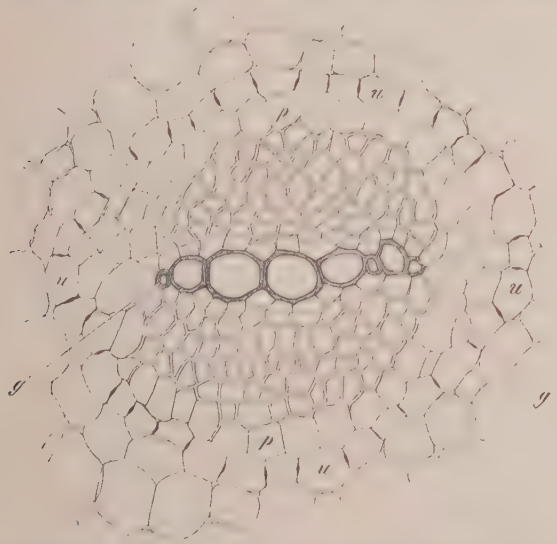

FIG. 163.—Ranunculus fluitans. Cross-section through the vascular bundle of a strong old adventitious root (225). *u* endodermis, *p* pericambium, *g* external primordial vessels of the diarch uniseriate xylem *g*—*g*; between *g*—*g* and *p* is the phloem.

(Brassica, Raphanus), Fumaria, Caryophyllaceæ, Vitis, Urtica, Umbelliferæ (Anthriscus Cerefolium, Fœniculum, Petroselinum sativum, Carum Carvi, Coriandrum, Daucus, Pastinaca sativa v. Tieghem), Chenopodiaceæ (Beta, Atriplex, Spinacia), Mirabilis, Centranthus, and Valeriana, and in Tagetes erecta among Compositae; tetrarch xylems as a rule occur in the investigated Cucurbitaceæ (Cucumis, Cucurbita, Lagenaria, Luffa), Euphorbiaceæ (Euphorbia, Ricinus, Mercurialis sp.), Tropæolum majus, Convolvulus tricolor; generally the numbers 2 and 4 appear to be predominant. But on the other hand considerable differences between the forms investigated occur in the case of the higher numbers of the Cupuliferæ above

[1] Compare van Tieghem, *l. c.* p. 223. In the case cited it was doubtful whether the main root or a strongly developed lateral root was in question.

mentioned; and among the Papilionaceæ, of which more numerous representatives have been investigated than of other families, a considerable variety of the conditions in question is to be recorded; as a rule the xylem-plates are diarch in Lupinus varius and Trigonella, triarch in Pisum sativum, Lathyrus sativus, Orobus vernus, Vicia sativa, Ervilia villosa, Ervum Lens, Hedysarum coronarium, Onobrychis sativa, and Medicago sativa; tetrarch in Phaseolus, Dolichos lignosus, and Cicer arietinum; lastly, higher numbers than four occur, as mentioned above, in Vicia Faba.

In the *branches of the root* the numbers remain as a rule the same, or diminish if they were greater than two. In *subsidiary* roots springing from the stem they often increase, in correspondence with the thickness of the roots; amounting, for example, to 7, 9, 11 in Cucurbita maxima, 5, 6, 8 in Lagenaria and Luffa (van Tieghem), 4–5 in Phaseolus, 5–8 in Valeriana; the adventitious roots on the rhizome of Nymphæa alba have 6–10 rays; in Nuphar luteum there are as many as 27; in an aerial root of Clusia flava van Tieghem found 13 rays, and so on. The converse case, however, also occurs; there is a diarch xylem-plate in all the adventitious and lateral roots of Tropæolum majus, the main root being tetrarch.

The orientation of the parts in the cases investigated is such that, in the case of diarch and tetrarch structure of the *main* root, the surface or one of the two intersecting surfaces of the xylem-plates always coincides with the median plane of the two cotyledons, which diverge at an angle of 180°. In the triarch main roots of Pisum, and the other triarch Papilionaceæ mentioned, the planes of two xylem-plates fall according to van Tieghem in the median planes of the two cotyledons, which only diverge at an angle of 120°. For higher numbers exact statements are wanting. In *all Phanerogams* the plane of the diarch xylem-plates of *lateral* roots always lies in the median plane of the main axis from which they arise, and the same applies, so far as investigated, to one of the planes in tetrarch xylems.

The original structure of the individual bands of tissue shows—within the general plan of structure of root-bundles—few peculiarities characteristic of Dicotyledons. As regards the xylem-plates the usually very gradual increase of the width of the vessels in the centripetal direction is worthy of remark. Only as an exception, in the polyarch subsidiary roots on the rhizome of Primula Auricula and Nymphæaceæ does the case usual in Monocotyledons occur, namely, that the short row of vessels, which does not reach to the centre, consists of a few narrow peripheral vessels, and then of one or several which are very wide (Fig. 164). In most cases belonging to this series the one- or few-rowed plates constitute radial bands, narrow in cross-section, separated by relatively very broad interstices. These bands either meet in the middle, or they are separated, or connected together, by means of a parenchymatous axial strand. In stout polyarch subsidiary roots, and in the upper part of stout main-roots, where they pass over into the hypocotyledonary stem, this axial parenchymatous mass, the 'pith' of the root, is of considerable thickness. Rarely, among Dicotyledons, the axial parenchyma connecting the xylem-rays is represented by a strand of sclerenchymatous fibres, e. g. in the subsidiary roots of Stachys sylvatica, Mentha aquatica, and Hedera Helix (v. Tieghem).

A peculiarity, which so far as I am aware only occurs among Dicotyledons, is the presence of a bundle of sclerenchymatous fibres, roughly crescent-shaped as seen in cross-section, on the outside of the phloem-groups of triarch and tetrarch roots of

Papilionaceæ (Pisum, Phaseolus). The fibrous bundle lies inside the pericambium. In other respects the phloem still requires more exact histological investigation in these cases.

In all roots of Dicotyledons investigated a pericambium, consisting of one, or in many cases of several layers, completely surrounds the xylem-plates. Those peculiarities of its structure which are related to the development of lateral roots, the resin-canals which sometimes occur in it, and other points connected with it, will have to be discussed below (Sects. 117 and 133).

This original structure of the roots of Dicotyledons is, however, permanent in but few cases; in most cases, and in many species immediately after its origination, it is altered by the secondary growth in thickness, starting from the inside of the phloem-rays, of which we shall treat in Chap. XIV; comp. Fig. 165. Hence result essential and actual differences from other roots, especially those of Ferns and Monocotyledons, in which, with the exception of many roots of Dracæna [1], these secondary changes are wanting. It must, however, be expressly stated that the changes due to secondary growth in thickness occur in by no means all roots of Dicotyledons, and thus do not establish any generally valid distinction between these and the others. Apart from those cases where, as in the subsidiary roots of Stachys silvatica, Mentha aquatica, Lysimachia nummularia, Myriophyllum, and Hippuris, the secondary growth in thickness is infinitesimally small, and as such even doubtful, because in other cases also the innermost vessels uniting the plates are developed very late, this secondary growth is completely absent in a number of subsidiary roots. For instance in those of Gunnera [2], the Nymphæaceæ, Ficaria ranunculoides, and Primula Auricula, to which cases it may be anticipated that more extended investigation will add others. The fact that a rudimentary secondary growth in thickness occurs at the points of insertion of the roots in question (in Ficaria and Nuphar [3]) has no effect on the condition of their much greater portion.

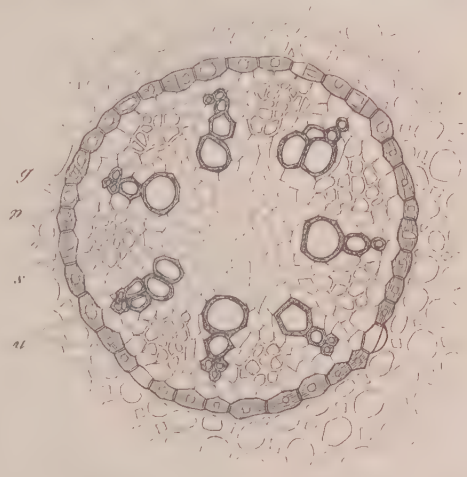

FIG. 164.—Primula Auricula (225). Cross-section through the heptarch vascular bundle of an adventitious root and its surrounding tissue. *p* pericambium; *p* the external primordial vessels of the xylem rays, which alternate with the same number of phloem groups *s*, and are separated from the latter by thin-walled parenchyma; *u* endodermis, outside which is tolerably thick-walled cortical parenchyma, with intercellular spaces quadrangular in cross-section.

The fact that in roots of Dicotyledons sclerosis of the endodermis but rarely occurs no doubt stands in the closest relation with the occurrence of secondary growth. Such sclerosis, however, occurs for example in the adventitious roots on the rhizome of Primula Auricula and Ranunculus repens; comp. Figs. 164 and 165.

[1] Compare Caspary, Pringsheim's Jahrb. I. p. 446.—Falkenberg, *l. c.* p. 197.
[2] Reinke, Morpholog. Abhandl. p. 58. [3] Van Tieghem, *l. c.* p. 266, &c.

2. The axial bundle of the root in the *Gymnosperms*[1] is in general similarly constructed to the ordinary one of Dicotyledons. Its original structure is always altered very early by secondary growth from the cambium; the sclerenchymatous fibres in the periphery of the phloem region of Dion described by Reinke may have owed their origin to this. Over the angles of the xylem-plates the pericambium is single-layered in Taxus, Thuja, and Biota; many-layered (from 3 and 4 to 7 cell-layers thick) in species of Podocarpus, Pinus, and in the Cycadeæ investigated.

The xylem-plates consist at their outer corners of tracheides, with the fibrous thickenings generally characteristic of this region; in their internal, later developed portion they consist of pitted tracheides, such as are characteristic of the wood of Gymnosperms.

Among the Coniferæ the Cupressineæ and Taxineæ have diametral and diarch xylem-plates in roots of all degrees, or more rarely triarch ones. In the Abietineæ higher

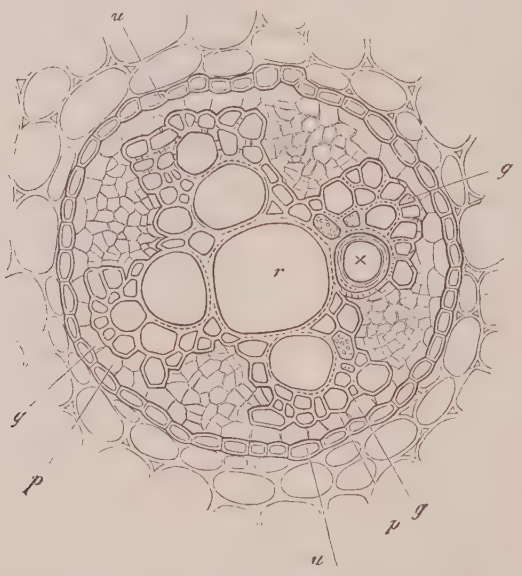

FIG. 165 (145).—Ranunculus repens. Cross-section through the vascular bundle of an old adventitious root. *u* endodermis, *p* pericambial layer, *g* external primordial vessels of the tetrarch xylem, *r* large axial pitted vessel. In the pitted vessel × surface-view of a roundly perforated cross-wall. A narrow zone of secondary wood has been deposited on the primary xylem plates extending from *g* to *r*; the cells between this and the phloem groups are tangentially divided; cf. Chapter XIV.

numbers and with them greater individual variations are the rule, though here no constant relation exists in the main root between these variations and the number of the cotyledons, which, as is well known, is likewise variable and always more than two. In Abies excelsa, for example, van Tieghem found in 13 seedlings a triarch root-bundle, the cotyledons numbering 7, 8, 9, or 10; in a specimen with 6 cotyledons the bundle was diarch, in one with 8, tetrarch. The numerous investigations of the observer mentioned established similar relations for the species of the genus Pinus in the narrowest sense (P. Pinea, halepensis, sylvestris, &c.). The number of the xylem-plates here amounts

[1] See van Tieghem, *l. c.*—Strasburger, Coniferen und Gnetaceen, pp. 340, 360, &c.—Mettenius, Beitr. z. Anatomie d. Cycadeen, p. 595, &c.—Reinke, Morpholog. Abhandl. I.

to 3–6, rarely 7. They are distinguished from those of the closely-related Abietineæ by their form, which may be compared to that of a Y. Each of them is, literally speaking, diarch; and begins externally with two rows of about five narrow tracheides, touching the pericambium at two separate points; they converge towards the inside and abut on each other. From their point of junction a radial row of tracheides, 1–2 layers thick, extends in the centripetal direction, without reaching the centre of the root. In the angle of the Y lies a resin-canal surrounded by delicate cells.

The roots of Ephedra which have been investigated have diametrally diarch xylem-plates.

Among the Cycadeæ the xylem in the subsidiary and branch-roots, which have been investigated in numerous species, is usually diametrally diarch, the two original plates meeting in the middle, or being separated by parenchyma. The same holds good for the investigated main roots of Cycas revoluta and Zamia furfuracea. More rarely, in the thick subsidiary roots of usually diarch species, the bundles are three-rayed. In a hybrid Ceratozamia van Tieghem found three or four xylem-plates, and in a specimen of Zamia muricata Mettenius found six in the main root. In the subsidiary roots of Cycas revoluta, when the centripetal development of the plate is already advanced, some scattered narrow reticulated vessels appear at the sides of its peripheral corners, as if secondarily; whether these constitute the first beginnings of the secondary growth remains to be decided.

3. Among the Monocotyledons there are first of all many thin main roots of the seedling, which in the structure of their axial vascular bundle are indistinguishable from those of Dicotyledons and Gymnosperms. In the case of Allium Cepa, with a diametrally diarch, and sometimes triarch xylem-plate, this has already been mentioned above; A. Porrum and Lilium Martagon are characterised by a similar structure of the main-root, Tulipa Gesneriana shows the deviation that its pericambium consists of two layers instead of one. Bulbine annua has three xylem-plates, which do not meet; Iris Monnieri has four. The weaker roots of all degrees are essentially similar to those just described.

Stouter main-roots, such even as those of species of Asphodelus, Canna, and Asparagus officinalis, and then those of the Palms (Phœnix, Seaforthia elegans), and above all the subsidiary roots springing from the stem (which in this class, as is well known, usually far exceed the main-roots in thickness), though in the great majority of cases they maintain the typical plan of structure, yet become polyarch as their bundles increase in bulk, and also show a more varied differentiation, due to differences of many kinds in the structure of the tissue-elements. Comp. Figs. 166, 167, 168.

First of all, as regards the number, arrangement, and form of the groups of tissue of these typical roots of Monocotyledons, the number of the xylem and phloem rays rises from 5–10 up to 20, 50, and more. The thick roots of Iris, Asparagus, Smilax (Sarsaparilla), Palms [1], &c., are examples of a high degree of polyarchy. The phloem-bands are always small, consisting of relatively few elements, their cross-section being roundish or radially elongated. The xylem-bands, consisting of one or a few rows of elements, usually begin at the periphery with a short uninterrupted radial band of narrow tracheæ, which become gradually wider towards the inside. These are suddenly followed in the centripetal direction by one or a few, very wide, reticulated or pitted vessels. The latter are usually separated from the peripheral

[1] Von Mohl, Palm. Structura, Diplothemium maritimum, Tab. I.

part of the row by one or more layers of interstitial cells. In the thicker polyarch bundles these large vessels are often confined to certain rows, while in the others, which alternate irregularly with the former, they are absent; or the case frequently

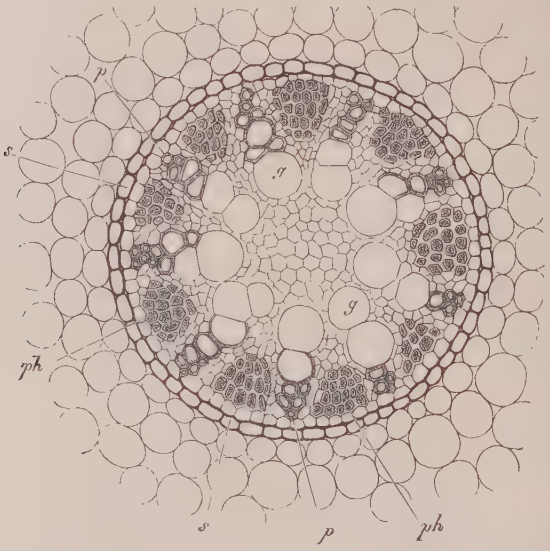

FIG. 166.—Acorus Calamus. Cross-section through a vascular bundle and the neighbouring part of the cortex of an adventitious root. *s* endodermis; *p*, *p* narrow primitive vessels; *g* larger internal vessels, not yet completely developed; *ph* phloem-groups. From Sachs' Textbook.

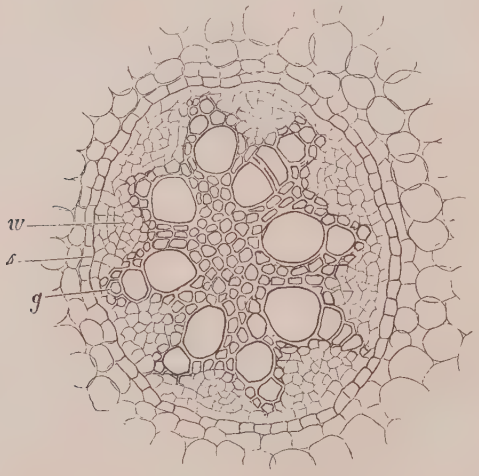

FIG. 167.—Very thin cross-section through the vascular bundle of an older adventitious root of the same plant (145). *s* endodermis, *g* primitive vessels, *w* phloem groups. The axial mass of cells, which is still thin-walled in Fig. 166, is here sclerotic, and the internal vessels are completely developed.

occurs that two neighbouring rows converge at an acute angle towards a large vessel, forming in cross-section the figure of a V, in the angle of which the large vessel lies. Xylem-plates do, however, occur among Monocotyledons also, in which the elements

become wider quite gradually in centripetal order, e.g. in many Orchids, as Stanhopea sp., Epidendron ciliare, &c. Here also the number of the vessels of a plate following one another in the radial direction is small, on the average 4-6, not unfrequently still fewer. In the Carices investigated the row usually consists of a single narrow peripheral vessel, or two lying side by side in the tangential direction, and one wide internal pitted vessel, the latter being separated from the former by at least three layers of parenchymatous cells. A second narrow pitted vessel may lie between the two. The peripheral vessels often occur without the corresponding wide one, so that a row can no longer be spoken of.

In smaller roots or bundles, as in the main roots mentioned above, the weaker roots of all degrees among the Grasses (Secale, Triticum), and in weak adventitious roots of Tradescantia virginica, the xylem-rows either meet in the middle of the bundle, or converge towards one or two wide vessels passing through the centre of the bundle, which originate very early, but attain their development very late. The xylem-rows sometimes come into direct contact with these, or are sometimes separated from them by a few interstitial cells. In the thicker typical roots of Monocotyledons the radial xylem-plates do not nearly reach the centre. The latter is occupied by a thick cylinder of parenchyma or sclerenchyma, at the circumference of which the system of xylem-plates often forms a relatively narrow ring.

In the great majority of roots of Monocotyledons the xylem-ring is surrounded on the outside by an uninterrupted pericambium, which is one layer thick over the xylem-plates, and the outside of which borders on the endodermis. It rarely consists of two layers over the xylem-plates, as in the main roots of Tulipa Gesneriana mentioned above, and in roots of Sarsaparilla. All the roots of Gramineæ investigated form a remarkable exception to this rule (Oryza [1], Secale, Triticum, Zea, Coix, Sorghum, Hordeum, and Paspalum spec. [2]), as in these the pericambium is, as a rule, interrupted by the rows of vessels which thus border directly on the endodermis. Even here, however, a small pericambial cell often lies between the endodermis and the outermost vessels, e.g. in Maize. The same occurs among the Cyperaceæ in species of Carex. In certain cases the narrow pitted vessel borders closely on the endodermis, e.g. in C. fœnea, folliculata, divulsa, and hirta; or both this and the usual arrangement, in which a pericambial cell is present outside the vessel, may occur in different parts of one and the same cross-section. According to van Tieghem, other species of Carex, such as C. brizoides, only show the latter typical arrangement; the same is the case in species of Cyperus, as C. longus and C. alternifolius.

In these typical roots the structure of the single tissue-elements shows a variety of individual differences, both as regards the vessels, and no doubt the sieve-tubes also, though the latter in most cases still require more accurate investigation. Into these differences we cannot here enter at all minutely. The mass of cells, forming simultaneously longitudinal and concentric rows between and inside the xylem-plates, shows sometimes a typically parenchymatous, sometimes a typically sclerenchymatous structure, or a form intermediate between the two. And indeed these peculiarities either extend uniformly to the whole interstitial mass of tissue in question, or are

[1] Nägeli und Leitgeb, *l.c.*

[2] Van Tieghem, *l.c.* [See further, Klinge, Vergl. hist. Unters. d. Gramineen u. Cyperaceen-wurzeln, Mém. de l'Acad. Imp. St. Pétersb. VII. Sér. Tom. XXVI. No. 12, 1879.]

different in certain zones and groups. Of the combinations which are here possible the following usually occur: (1) the entire interstitial mass of cells, including the cylindrical axial portion, remains thin-walled and parenchymatous, e. g. adventitious roots of Tradescantia virginiana, Curcuma longa, and Clivia nobilis (Acorus Calamus is intermediate, i. e. its parenchyma has very strong walls). (2) The whole mass of cells mentioned becomes sclerenchymatous, e. g. Carex divulsa, Cyperus alternifolius, and no doubt most adventitious roots of Cyperaceæ and Grasses; also Curculigo recurvata. (3) The tracts of cells between the xylem- and phloem-plates are sclerenchymatous, forming together with them a dense firm ring around an axial strand of parenchyma, with intercellular spaces containing air: e. g. roots of Smilax (Sarsaparilla) with very extensive parenchyma containing abundance of starch, most aerial roots of Orchidaceæ (e. g. Epidendron ciliare, Oncidium sphegiferum), and many Palm roots (cf. Mohl, *l. c.*), in which scattered sclerenchymatous fibres may occur again inside the axial thin-walled parenchyma, e. g. Chamædorea elegans.

The pericambium remains in most cases thin-walled and parenchymatous, even where it borders on sclerenchyma, though it may itself eventually be involved in the sclerosis, either wholly or in part; the former, for example, is the case in Sarsaparilla roots, the latter among Orchids, e. g. Epidendron ciliare, where opposite each xylem-plate two rows of its cells usually remain very delicate, while the others, like those adjoining them on the inside, become greatly thickened. The usually one-sided sclerosis of the endodermis, which is very frequent, though by no means universally distributed among long-lived Monocotyledonous roots, has been discussed in Sect. 27.

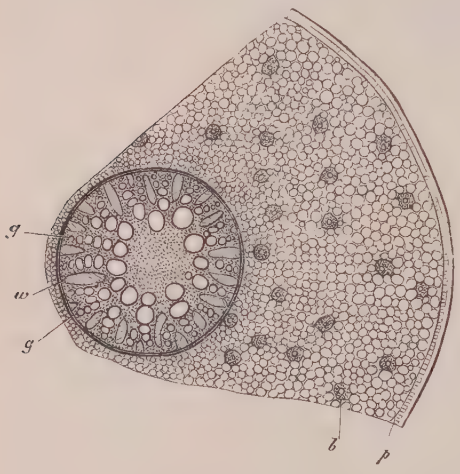

FIG. 168.—Philodendron Imbe Hort. Halens. Cross-section through a thick subsidiary root, slightly magnified. The axial vascular bundle, and on the right the entire cortex, are shown; *g* external limit of the xylem-rows. The obliquely shaded radial bands *w* are the phloem-groups; *p* periderm; *b* fibrous bundle surrounding an intercellular passage containing latex.

Deviations from the type of structure of Monocotyledonous roots hitherto considered occur in different degrees as regards the arrangement of the forms and regions of tissue, though their structural conditions remain the same.

In thick root-bundles, some or all of whose xylem-plates converge in pairs in the form of a V, the groups of phloem lying inside a V are often smaller than those between two V's. The latter are frequently large, radially-placed plates, while the former are roundish groups. This occurs in an exquisite form in the aerial roots of an Aroid cultivated in Halle under the name of Philodendron Imbe (Fig. 168), and also in Palms; cf. Mohl's figure of Diplothemium maritimum already cited. In Chamædorea elegans this inequality goes further. In the corner of the V lies a small roundish group of phloem; between every two V's a similar group lies towards

the outside, while further inside a second occurs, which is elliptical in cross-section, and is separated from the outer group by interstitial sclerenchyma, in which vessels frequently lie. Thus both an inner and an outer row of phloem-groups are here present in the otherwise typical bundle.

It has been mentioned above that the xylem-plates not uncommonly converge towards one or two axial vessels, though it may be without coming into immediate contact with them. Such axial vessels frequently occur isolated, in the middle of a thick parenchymatous or fibrous cylinder, and are separated from the inner edges of the radial plates by many layers of cells. This kind of structure is found here and there as an individual peculiarity of many roots, as for example in the Sarsaparilla of Veracruz[1]; in Carex folliculata I found, on the same stock, roots of the structure usual in Carex, with a thick dense sclerotic axial-cylinder, and others in which the middle of the latter is traversed by about 5 moderately large, prismatic, pitted vessels, which are in contact with one another.

These trifling forms of deviation constitute the transition to those more conspicuous cases, in which numerous vessels, as well as groups of sieve-tubes, occur scattered in the whole of the cylinder inside the radial ring, a phenomenon which is characteristic of the thick adventitious roots of many epiphytic Aroideæ, of those Musaceæ which have been investigated, of the Dracæneæ, Pandaneæ, (Pandanus, Freycinetia, Cyclanthus), and of the Palms Iriartea exorrhiza and I. præmorsa.

All the investigated roots of terrestrial Aroideæ, as well as those of many epiphytic species, present the usual typical structure; but in the thick aerial roots of other forms, scattered wide vessels, and very large sieve-tubes, isolated or occurring in pairs, and accompanied by cambiform tissue, are distributed throughout the wide and constantly sclerenchymatous cylinder inside the radial ring. The two kinds of elements do not lie in the radial rows; Tornelia fragrans, Heteropsis ovata, Monstera surinamensis, Adansonii, Raphidophora angustifolia, Scindapsus pictus, Philodendron micans, and Anthurium digitatum[2], are examples of this structure.

The same occurs in species of Strelitzia, and no doubt in other Musaceæ[3].

Essentially the same arrangement is present in roots of Dracænæ and Pandaneæ, with the sole difference that the axial tissue in which vessels and sieve-tubes are distributed is not homogeneous, but around the vessels and small phloem-groups consists of sclerenchymatous fibres, while between them it is formed of parenchyma, in which, in the case of Pandanus, lie wide intercellular passages containing air and scattered bundles of fibres. The ring has likewise sclerotic interstitial tissue between the radial xylem- and phloem-groups, the number of which even in moderately thick (1.5 cm.) roots of Pandanus amounts to nearly 200 of each. The cross-section of such roots therefore presents first the typical, relatively narrow ring, surrounded by a many-layered pericambium and an endodermis, and then, inside this, a wide space filled by parenchyma, in which numerous thick strands run longitudinally. Each of these strands consists of a many-layered mass of sclerenchymatous fibres, in which are enclosed one or more isolated wide vessels or groups of them, and one or more small phloem-groups separated from the vessels, while more rarely only one, or neither of the two forms of tubes are present. The position of the two in the strand varies irregularly. The distribution of the strands in the parenchyma appears in equivalent roots to be somewhat different according to the species. Among

[1] See Berg, Atlas d. pharmac. Waarenkunde, Taf. III. g.

[2] Van Tieghem, *l.c.* p. 149.

[3] Compare Wittmack, Musa Ensete, Halle (Linnæa), 1867, p. 62.

the Pandaneæ, for example, I find them, as seen in cross-sections, isolated and irregularly distributed, in the thickest roots of Freycinetia nitida of the Berlin Gardens; in Pandanus pygmæus (graminifolius of gardens) they are arranged in transverse rows (parallel to a diameter), which are separated from one another by broader bands of parenchyma. In P. odoratissimus, two or more strands separated by narrow bands of parenchyma are placed together in groups, and the groups scattered between broader masses of parenchyma. As the thickness of the roots diminishes the conditions of structure described become simplified. A branch-root of Pandanus pygmæus, 1–2 mm. in thickness, has, for example, inside the radial ring about 2–3 large vessels, and the same number of phloem-groups, enclosed in homogeneous fibrous sclerenchyma, which is directly continued into the ring. Branch-roots of Dracæna reflexa about 1 mm. in thickness have a thoroughly typical structure, the radial ring surrounds a thin-walled axial cylinder of parenchyma. It is only in thicker roots that an irregularly placed strand of sclerenchyma containing vessels appears, such strands becoming very numerous as the roots increase in thickness.

The roots of Iriartea, finally, which are an inch in thickness, are distinguished from those last described, first by the fact that their bulky vascular mass is not cylindrical, but deeply furrowed, having in cross-section the form of a star with about ten blunt and usually bifid rays; further by the fact that the radial ring also is divided up into sclerenchymatous bundles, enclosing the vessels and phloem-groups, and radial bands of parenchyma, which are sometimes narrow, 1–2 layers in thickness, sometimes many-layered, and which separate the bundles from one another. The middle of the star also consists mainly of thin-walled parenchyma, often with lacunæ, which is directly continued into the radial bands of the ring, and in which bundles of sclerenchyma, each containing one or more vessels and phloem-groups, lie scattered. Inside each sclerenchymatous bundle the vessels are surrounded by 1–2 layers of parenchymatous cells, those of them which belong to the ring standing in direct connection with the many-layered pericambium. An endodermis, which is thickened here and there, appears according to Mohl's figure to surround the star. Finally, in the entire parenchyma, both of the star and of the cortex which surrounds it, numerous small bundles of sclerenchymatous fibres lie, each enclosing in its centre 1-2 thin-walled elongated elements (perhaps sieve-tubes?). The xylem-plates in the ring appear short and irregular in cross-section, their radial arrangement and alternation with the phloem-plates is according to Mohl's figure often indistinct, though in general to be recognised. The development of the elements, both in Iriartea (Karsten) and in the roots of Pandanus, begins at the periphery of the ring, and in general proceeds centripetally. According to all these phenomena, the series of large roots just described are immediately connected with the type of Monocotyledons as special cases, in which the anatomical differentiation becomes more varied, with the more considerable size.

The system of bundles, which traverses the tuberous roots mentioned at p. 233, is entirely different in structure from the bundles last mentioned. In Dioscorea and Sedum all the bundles are typically collateral. The same holds good for the Ophrydeæ, with the limitation that the vessels are only very sparingly developed. Each bundle is surrounded by a separate endodermis.

4. In the *Filices* in the widest sense, the Marsiliaceæ, and the Equiseta, with a few exceptions to be mentioned below, the axial cylindrical bundle of the roots does not deviate in its differentiation from the types hitherto regarded[1]. Its xylem is in the great majority of cases, with the exception of the Marattiaceæ, diametrally diarch, beginning externally on each side with some narrow, fibrously-thickened tracheides lying side by side, which are succeeded in the centripetal direction by one or a few rows of wider, often large scalariform tracheides, of the structure usual in Ferns; (true vessels only occur in Athyrium Filix femina[2]). Cf. Fig. 169. In Botrychium, the

[1] Compare Nägeli und Leitgeb, van Tieghem, Russow, *ll. cc.*

[2] Compare p. 165.

tracheides, which form several rows, are of a different structure, similar to that described in the case of the stem and leaf at p. 346, and are all of approximately equal and relatively small width. Triarch and tetrarch bundles sometimes occur in thick roots of species, which are usually diarch; triarch-bundles have been observed in Pilularia, Equisetum, Botrychium, Blechnum brasiliense, and Cyathea medullaris, tetrarch in Equisetum, the Blechnum above mentioned, and Cyathea. In the species of Trichomanes[1] investigated triarch to octarch bundles usually occur, diarch bundles being rare, while, on the other hand, the latter are characteristic of the roots of Hymenophyllum. On the monarch bundles of some species of Trichomanes, see below.

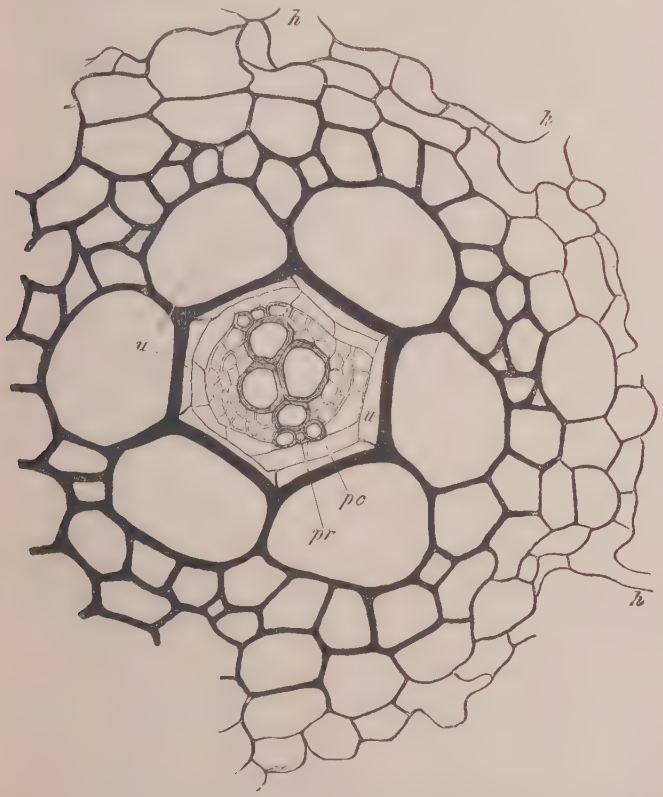

FIG. 169.—Adiantum Moritzianum (225). Old root, cross-section. *h*—*h* hairs of the epidermis cut through, *u* endodermis, *pc* pericambium, *pr* primitive tracheides of the diarch xylem alternating with two phloem groups.

The xylem-plates are in most cases united in the middle, in the thinner bundles often by means of a very large vessel (e. g. Equisetum), or of a row consisting of two large vessels, crossing the diametral pair of plates at right angles (Fig. 169). In other respects various subordinate differences of form occur, e. g. a regularly elliptical cross-section of the diametrally united plate in Osmunda, Todea, &c., &c.

The arrangement of the phloem-groups corresponds to the general plan of

[1] Mettenius, Hymenophyllaceen, *l. c.* p. 420.—Russow, *l. c.* p. 95.

root-structure; their histological peculiarities are essentially similar to those of the stem of the same plant, and like the latter still require more exact investigation.

The pericambium appears, as a rule, as a single layer all round, but it also occurs with two layers; this is the case only outside the phloem-groups in Aspidium Thelypteris, and all round in Polypodium ireoides[1]; in Osmunda and Todea there are several layers all round. In the Equiseta, in contrast to the other forms belonging to this series, all the cells of the pericambium stand precisely in front of those of the endodermal sheath, and together with these have arisen from the division of the innermost cortical layer. In the other vascular Cryptogams the latter forms the endodermis only, while the pericambium originates by tangential division of the plerome-cylinder surrounded by the cortex.

In the endodermis, apart from various subordinate differences of form, the cells lying in front of the corners of the xylem-plates are the initial cells of the lateral roots, and are often distinguished from the others by their more considerable size. The structure of the endodermis is otherwise essentially the same as in the bundles of the stems of the same plants.

In the roots of Cryptogams, the orientation of the diametrally diarch xylem-plates is always such that their surface cuts the median plane of the next higher order of ramification at right angles. Those arising on the stem appear, according to species, either to have the like orientation with reference to its median plane, or to have their surface coincident with the median plane of the stem.

The axial root-bundles of the Marattiaceæ[2] are distinguished from those of the other Ferns, with which their structure otherwise agrees, by their tetrarch or polyarch xylem[3]. The number and length of the radial plates increases, in the same species, with the thickness of the roots; the former may amount to 18–20. In the thicker roots we frequently find them converging in pairs, and as seen in cross-section united to form the figure V. In the roots occurring above the ground the xylem-plates do not reach to the middle of the bundle; in the thin, 4–5 rayed branches underground, they meet, according to Russow, in the middle.

The very thin root-bundle of Azolla[4], which differs in its development from that of the Ferns, has, according to Strasburger, a usually triarch xylem, consisting only of spiral tracheides. Besides this there are only some inconspicuous elements lying inside the pericambium, and constituting a doubtful phloem.

Sect. 109. A structure departing from the general radial type of root occurs in the rhizophores of Selaginellæ[5], in the true roots of the same plants, in the thinner roots of Lycopodia, and in the roots of Isoetes and Ophioglossum: with the exception of the rhizophore of Selaginella Kraussiana, the peculiarity of this structure consists in the fact that the usually monarch xylem either occupies one side of the bundle, the phloem lying on the other—the arrangement being thus collateral—or that the former is at least strongly approximated to one edge of the phloem which surrounds it. Most roots or rhizophores belonging to this series are dichotomously

[1] Van Tieghem, *l. c.*—Compare also Nägeli und Leitgeb, p. 83.
[2] Meyen, Haarlemer Preisschrift (1836), Tab. VIII.
[3] [Cf. Holle, Königl. Ges. d. Wiss. zu Gött. Jan. 8, 1876.]
[4] Strasburger, Ueber Azolla, p. 48.
[5] [M. Treub, Recherches sur les organes de la Vég. du Selaginella Martensii. Leyden. 1877.]

branched, and show a definite orientation of the parts of the bundle in the successive bifurcations. The structure in question might therefore be regarded as characteristic of dichotomous roots, if it were not that those of Ophioglossum are always entirely unbranched[1], for there is no basis of fact for van Tieghem's supposition, according to which this unbranched root would be the favoured branch of a root which has already undergone bifurcation while still inside the cortex of the stem which produces it, its other branch not coming to development.

Among the dichotomous rhizophores[2] and roots of the Selaginellæ, in the first place, the rhizophores of S. Kraussiana are distinguished by cylindrical vascular bundles, in which the middle of the central and centrifugally developing xylem is occupied by the narrow primitive tracheides, while the periphery is formed of wider scalariform tracheides. The phloem completely surrounds the xylem as a many-layered small-celled zone; histologically it still requires more exact investigation[3]. To form the bundles of the first pair of roots, the bundle of the rhizophore is uniformly severed into two halves, in which a group of narrow primitive tracheides occupies one edge of the xylem, while the development of the elements proceeds from this point towards the other broader side. The xylem is thus monarch, similar to the usual collateral bundles, from which those in question are distinguished by the fact that the phloem completely surrounds the whole xylem.

The structure last described belongs to all the investigated roots of Selaginella, and to the rhizophores of S. Martensii. These bundles also divide at the dichotomies in such a manner that the plane of division passes through the primitive group and the edge of the xylem lying diametrically opposite to it. In primary axes arising from the stem, the orientation of the bundles with a unilateral group of primitive tracheides is such that that group faces the base of the stem. In the dichotomous branches it always lies on the inner side, turned towards the other branch of the pair. At every bifurcation therefore each bundle proceeding from the division of the main-bundle undergoes a torsion of 90°, and indeed this takes place gradually inside the main axis, in such a way that the two bundles run on side by side from the point where they separate, which is above the point of bifurcation of the root, as far down as the latter. Only in the first dichotomous branches of the rhizophore of S. Kraussiana does the same orientation come about without torsion.

The feeble bundles in the roots of *Isoetes*[4] show in the general structure of their unilaterally monarch xylem, and in its orientation in the dichotomous branches, the same behaviour as those of Selaginella. As regards the elementary composition of this part they are distinguished by the fact that it consists only of a few rows of annular and reticulated tracheides, without scalariform vessels. So far as investigations extend, the phloem is feebly developed, and confined to the side remote from the primitive tracheides; as seen in cross-section it has the form of a narrow crescent-shaped band, while its histological structure is indistinct. The position of the bundle in the root is from the first slightly eccentric, and in the dichotomous branches always approaches the other branch of the pair. The eccentricity, which is caused by a mainly one-sided extension of the cortex and of its large air-cavities, increases with the thickness of the roots. According to Mettenius' short statement[5], the structure of the xylem and the eccentric position of the bundle in the roots of *Phylloglossum* are similar to those in Isoetes. The bundle approaches that side of the always unbranched root which is basiscopic with reference to the stem.

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[1] Compare Holle, Botan. Zeitg. 1875. Holle's observations are not in agreement with van Tieghem's statement that the roots of Botrychium, with typically radial bundles, are dichotomous (p. 315).

[2] Nägeli und Leitgeb, *l. c.* p. 124.

[3] [Cf. Treub, *l. c.*]

[4] Hofmeister, Beiträge z. Kenntniss d. Gefässkryptogamen, I.—Nägeli und Leitgeb, *l. c.* p. 131.

[5] Botan. Zeitg. 1867, p. 99.

The thin roots of *Lycopodium*, already described at p. 350, are immediately related to the above.

Lastly, the roots of *Ophioglossum* are to be mentioned here[1]. In the circular cross-section of the axial bundle it may be seen that the half, which with reference to the parent axis is basiscopic (lower), is formed of tracheides, which are united together without intercellular cavities, and are similar to those of the stem (p. 346). The upper edge of the bundle is formed by a half-ring, usually two layers in thickness, of relatively large, wide sieve-tubes. Between this phloem and the xylem lie some layers,—numbering on the average three,—of delicate prismatic, narrower elements, destitute of starch, the sieve-tube nature of which is doubtful; as a rule a layer of delicate cells separates the xylem from the endodermis, while the sieve-tubes border immediately on the latter. According to van Tieghem the last statement often holds good also for the two middle tracheides of the lower edge. The development of the tracheides begins at one corner of the segment of the circle, and proceeds from this point round the convex edge, and from this again towards the phloem. The endodermis, like that of the stem, only differs from the other cortical parenchyma in the undulating bands on its radial walls.

4. *Imperfect and rudimentary Bundle-trunks.*

Sect. 110. The vascular bundles described above occur in land plants possessing foliage which is rich in chlorophyll, and also in the stems and leaves of parasites which contain no chlorophyll, or only traces of it, as in the Orobanches, Cuscutas, Lennoaceæ, &c. As indicated at p. 321, they are *ceteris paribus*, as a rule, all the more developed the greater the development of the leaf-surface.

Conversely, the development of the vascular bundle-system diminishes in every respect with that of the leaf-surface exposed to the air; and this is the case firstly with regard to its differentiation into individual bundles and their branches, as is clearly shown by its reduction to an axial strand in the stems of many submerged plants (cf. pp. 277, 321), and by its simplification in the submerged leaves of amphibious plants (p. 306); and secondly as regards the anatomical differentiation of the individual bundle. In the latter, while the plan of structure remains the same, a diminution of the essential tissue-forms may be recognised, as, for example, the comparison of the bundles in the stem and root of Ranunculus repens (Figs. 152, 165) with those of R. fluitans (Figs. 153, 163) teaches; and in fact the diminution is chiefly in the xylem, while the phloem remains the same, or is less reduced. Further, as the characteristic elements, and especially the tracheæ, progressively diminish, deviations from their usual typical arrangement also occur. Again, there may be complete disappearance of the tracheal elements, and finally of the sieve-tubes also, so that the entire bundle is replaced by a strand of uniform elongated cells. Lastly, we find the absence even of any rudimentary indication of a vascular bundle, as in the tiny swimming frond of the Wolffias, which is a large-celled mass of parenchyma, covered by an epidermis, which has stomata on the surface in contact with the air[2].

These cases of imperfectly developed bundles are to be contrasted with the complete ones hitherto considered. They are divided into two main categories, namely, those which originate as complete bundles, and then by disappearance of the xylem become more or less incomplete—being thus bundles with a transitory

[1] Van Tieghem, Russow, *l. c.*

[2] Hegelmaier, Lemnaceen, p. 31.

xylem,—and secondly, those which *remain* imperfect from the beginning. Both forms are connected step by step with the complete bundles by various intermediate forms, which have already often been mentioned above.

This especially holds good of those bundles which *become imperfect* by disappearance of the Tracheæ. In many herbaceous plants with collateral bundles an intercellular passage appears in place of the primitive vessels when the development of the tissues is complete, as was described at p. 327.

In a series of other plants, which are submerged or partly submerged aquatics, all the vessels in most of the bundles disappear at once throughout a long part of their course, after they have originated as annular or spiral vessels. In place of the xylem an intercellular canal (filled with water) occurs in the mature bundle, and on its walls the remnants of this thickened membrane may remain preserved. On the other hand, the phloem of the bundles is persistent, and, in many of the cases in question, very well developed. These phenomena present many variations according to the particular cases, and are especially conspicuous in the stems of the Potamogetons, and of the submerged plants connected with them, which have an axial bundle, or a very simple bundle-system [1]. Even in those among these forms in which, as in P. natans, distinct bundles of the leaf-trace and common bundles can be distinguished, the want of vessels on the one hand, and on the other hand the crowded position of the bundles, often gives the whole bundle-system a structure which at the first glance is difficult to decipher, and into this we here have to enter somewhat more minutely.

The course of the leaf-traces, and of the four cauline bundles in the stem of Potamogeton natans and perfoliatus, was described above at p. 272. All the bundles are at their origin collateral, with normal orientation.

In the node all their parts are persistent, and soon become irregularly united by anastomoses. In the whole internode, on the other hand, the entire xylem disappears from the bundles of the leaf-trace with the beginning of the more intense elongation, and is replaced by an approximately cylindrical narrow intercellular passage, bordered by narrow elongated cells [2]. In P. perfoliatus the same holds good also of the four cauline bundles; in P. natans, on the other hand, the few (1–3) reticulated and annular tracheæ of the latter are usually persistent. The phloem-portions of all the bundles are very well developed and persistent. All the bundles are further closely approximated to one another, being only separated by a few layers of parenchymatous cells containing abundant starch, and traversed by small groups of sclerenchymatous fibres. The bundles are grouped to form an axial strand, rectangular as seen in cross-section, which is marked off from the lacunose cortical parenchyma by an endodermis, which becomes sclerotic subsequently (Fig. 170). Inside this, one bundle faces each longer side of the rectangle; opposite one of these two sides is a larger bundle, the sympodial one, descending from the second leaf above: facing the other side is a somewhat smaller bundle, the median one of the next higher leaf, belonging to the internode. One of the lateral bundles of this leaf faces each of the shorter sides; the four cauline bundles face the four angles. A group of sieve-tubes lies at the

[1] Compare p. 277, and the literature there cited.
[2] A. B. Frank, Beitr. z. Pflanzenphysiol. p. 135.

outside of the wide intercellular passage of the sympodial bundle, while two somewhat smaller groups stand symmetrically right and left of the centre of its inner side. In the remaining bundles the intercellular passage or vascular group is bordered on the outside by an arched group of sieve-tubes.

In the other Potamogetons investigated (lucens, gramineus, densus, crispus, pectinatus, and pusillus), in Zanichellia, Althenia, Cymodocea, and Zostera, the tracheæ in the node are persistent, while those in the internode are all transitory. To every bundle an intercellular passage corresponds, which is surrounded on the outside by phloem. Where several bundles traverse the internode, they approach each other closely in a manner similar to that described for P. natans; in the case of the two leaf-trace bundles in the internodes of P. lucens and gramineus this goes so far, that

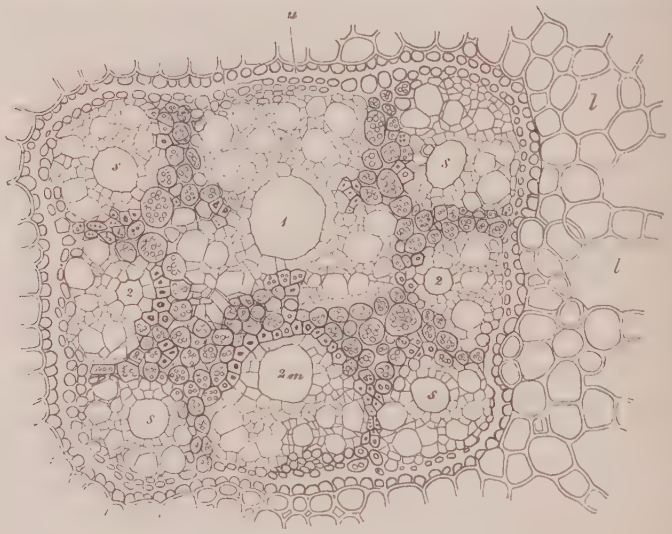

FIG. 170 (145).—Potamogeton natans. Axial mass of the internode, containing the vascular bundles; cross-section. *u* unilaterally thickened endodermis, containing starch; outside the latter lacunose cortical parenchyma, with abundant starch; *l* air-cavities. Explanation of the numerals at p. 272. The delicate groups of tissue of the numbered circles are the phloem; the wide meshes in the latter are the sieve-tubes of the bundles; the circles in which the numerals stand are the xylem portions, usually converted into cavities. Between the bundles is parenchyma containing starch, and sclerenchymatous fibres with a narrow lumen appearing as a darker point.

their intercellular passages, which are turned towards each other, are only separated by one layer of cells, or in most cases are united to form a single passage.

The single axial sympodial bundle, which (without cauline bundles) traverses the internode in the upright stem of P. pectinatus and pusillus (Fig. 171), has, in the manner of a concentric bundle, a central intercellular passage replacing the xylem-group, and this is completely surrounded by a relatively bulky phloem, containing large sieve-tubes, and externally limited by the endodermal sheath, which eventually becomes sclerotic.

The bundles in the stems of Zanichellia and Althenia behave quite similarly to the forms last mentioned, only with the difference that the phloem is very delicate and slightly developed, and consists of elongated cells with a few indistinct sieve-tubes. Elodea and Hydrilla, of which we shall speak later on, are also connected with these cases.

The vascular groups of Cymodocea æquorea[1] and Zostera behave, both in the nodes and in the internodes, like those of the Potamogetons. The intercellular canal derived from the xylem lies in the small peripheral bundles on the inner side; outside this is a radially elongated phloem-group containing two or three large sieve-tubes; in the thicker axial bundle the intercellular space occupies the middle, and in the case of Cymodocea has at its periphery four sieve-groups placed cross-wise in the transverse section; in Zostera it is completely surrounded by a broad phloem, as in Potamogeton pectinatus.

The small stems of the Hydrilleæ and of Aldrovanda vesiculosa constitute transitional forms between the bundles which *become* incomplete and those which *remain* rudimentary.

Elodea canadensis and Hydrilla verticillata have an axial bundle of essentially similar structure to that of Zanichellia. The one or two axial tracheæ present in the young rudiment of the stem, which send off a branch into each leaf, are incomplete from their first origin; their walls are only thickened with segments of rings, and disappear everywhere—even in the node—on the commencement of active extension[2]. According to Caspary, Aldrovanda shows an axial bundle of 8–9 annular tracheæ, which, together with their branches going to the leaves, are persistent in the nodes, but disappear in the internodes during extension, and are here replaced by a passage surrounded by delicate-walled elongated elements, which have not been more minutely investigated. Of bundles which *remain rudimentary*, those in the small stem of Ceratophyllum and Najas are immediately related to those just described. According to Sanio the former are bundles which are at all times destitute of vessels, and consist of a mantle of narrow sieve-tubes and elongated cells, between which lie several small intercellular passages, each produced by the absorption of a row of cells[3]; and inside this mantle are some layers of parenchyma, which surround an axial passage derived from the absorption of a multiseriate strand of cells. In the case of Najas the mature structure is similar to that of Elodea; sieve-tubes have not been described, and are doubtful; the axial canal arises from the absorption of a row of meristematic cells.

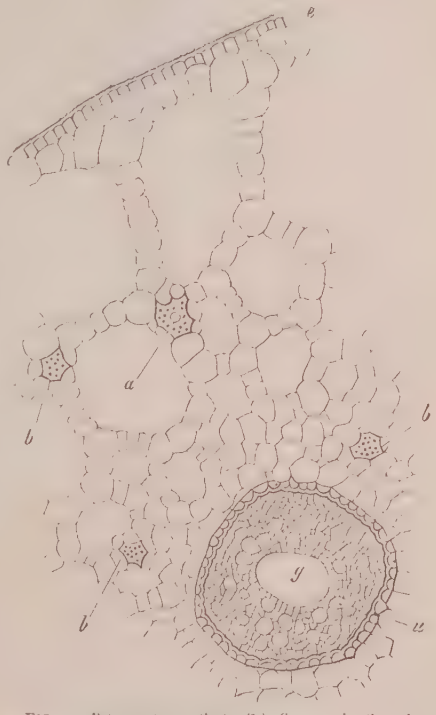

FIG. 171.—Potamogeton pectinatus (80). Cross-section through an internode of the upright stem. *x* intercellular passage replacing the xylem which has disappeared; *u* unilaterally thickened endodermis; between *u* and *e* the phloem, with wide sieve-tubes. Between *u* and the epidermis *e* is the lacunose cortex; *b* bundles of sclerenchymatous fibres; *a* a small bundle, with a small group of sieve-tubes in the middle.

[1] Compare Bornet, *l.c.* [2] Caspary, Sanio, *l.c.* (p. 278). [3] Compare Frank, Beitr. p. 143.

A structure deviating from that described occurs in the bundles of the small submerged stems of the floating Utricularias, the Lemnaceæ, the Podostemaceæ, Vallisneria spiralis, and in the rhizomes of Epipogon and Corallorhiza, which inhabit humus, all of these likewise remaining rudimentary.

In Utricularia vulgaris[1] an axial, approximately cylindrical bundle is present, and gives off a branch into each of the so-called leaves. Its smaller half, which with reference to the horizontally floating stem is the upper, consists of elongated prismatic cells, usually with flat ends and thick collenchymatous walls; the lower half consists chiefly of thinner-walled elements, namely, of wide sieve-tubes and numerous narrower prismatic cells. Near the boundary between the upper and lower half, but within the latter, next the centre, lies a single row of very long, wide tracheides, with their pointed ends applied to one another, showing alternately annular and spiral thickening. In the small and younger specimens no other tracheides occur. In very thick stems, on the other hand, I found a second single or double row of annular tracheides, lying at the side of those mentioned, near the periphery of the bundle. These are similar to the former in structure, but only about half as wide. Their development seems to take place very late. All the tracheides are persistent, no intercellular spaces whatever are present in the bundle.

The bundles in the frond of Lemna[2] consist in the native species of a thin row of annular tracheides, surrounded by one or a few layers of elongated cells. Spirodela polyrrhiza has several parallel rows of tracheides instead of one; in Lemna valdiviana, on the other hand, the development of tracheides is suppressed. The absence of any vascular bundles in the Wolffias has already been mentioned above.

The bundles of the Podostemaceæ, which are still much in want of accurate investigation, consist, according to Trécul's short statement[3], of a bundle of fibres and some small annular vessels, the latter being often absent in old stems and replaced by a cavity[4]. Vallisneria also requires more exact investigation[5].

The axial bundle in the rhizome of Corallorhiza contains in the middle two multiseriate strands of reticulated tracheides with narrow transverse meshes, and from these the simple bundles branch off for the distichous leaf-rudiments. It further consists of elongated, usually thin-walled, elements, which still require more exact investigation. In the rhizome of Epipogon the bundle consists, so far as investigations extend, only of uniform, moderately elongated cells, with oblique ends and thin walls.

In the *roots* of those aquatic plants, which in the stem possess incomplete or small bundles containing passages, the bundles, which here, it is true, are always feebly developed, may be complete, and provided with a persistent xylem constructed according to the radial type, e. g. Potamogeton lucens[6]. As a rule, however, they here also either become incomplete by disappearance of the vessels, intercellular passages appearing in their place, or they remain rudimentary.

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[1] Compare van Tieghem, Ann. Sci. Nat. 5 sér. tom. X. p. 54.

[2] Hegelmaier, Lemnaceen, p. 48. [3] Archives du Muséum d'Hist. Nat. tom. VI. p. 4

[4] [Compare Warming on Podostemaceæ, Mém. Acad. Roy. Copenhagen, 1881, &c.; also Cario, Tristicha hypnoides, Bot. Ztg. 1881, p. 25.]

[5] [Compare Franz Müller, die Entwickelung von Vallisneria spiralis, Hanstein's Abhandl. Bd. III. Heft. 4, 1878.]

[6] Van Tieghem, Ann. Sci. Nat. 5 sér. tom. XIII. p. 164, pl. VI.

The former process goes on as a rule more slowly in the roots, the vessels persist longer, than in the stems of the same plants. The structure of the root-bundle (pericambium, alternating xylem and phloem rays) here preserves its typical character, although the number both of the individual rays, and of the elements composing each of them, is low, the former being reduced to four or to two, the latter often to one. The mature root has therefore the typical bundle-structure, with the exception that in the place of the 2–4 xylem rays, each of which is represented by a vessel, and in place of the large central vessel, which in many cases unites the rays, an intercellular passage is present; e.g. Aponogeton, Alisma, Hydrocleis (van Tieghem).

In the root of Elodea canadensis, as in the stem of the same plant, the disappearance of the 4–5 peripheral vessels, and of the larger central vessel, which is separated from them by an annular layer of parenchyma, takes place immediately after their first, incomplete formation.

Among those root-bundles which on the other hand, *remain* rudimentary, those of Najas belong to this category. They consist of two layers of elongated delicate cells, and these surround an axial passage, which arises by the absorption of a row of meristematic cells.

In the root of Vallisneria, according to van Tieghem, there is only an annular layer of elongated cells enclosing an axial passage, and surrounded by the endodermis, and this constitutes the rudiment of the bundle. The delicate bundle in the root of species of Lemna shows in cross-section essentially the same structure; the middle is according to Hegelmaier occupied by a row of cells (not by a passage). Spirodela polyrrhiza shows the same character, but with the difference that the row of cells in the middle is developed into a persistent row of narrow annular tracheides.

II. Ends and Connections of the Vascular Bundles.

Sect. 111. The ends of the vascular bundles, as was shown above at Sect. 91, lie in the foliar expansions, and in the *cortex* of many plants, either as *internal* ends ceasing in the parenchyma, or forming anastomoses, or as *peripheral* ends at the edge or surface of the leaves; in the stems of Cyatheaceæ, described at p. 291, they also end in the interior of the pith.

With the ultimate degrees of ramification the thickness of the bundles usually diminishes, both the number and the size of their elements being reduced; at the extreme free ends they often, but not always, show a terminal dilatation. Xylem and phloem do not behave alike in this respect. Clearly characterised sieve-tubes are, it is true, often still present in the thicker bundles of the foliage leaf, e.g. in those of the leaf-nerves; in the last orders of ramification they are no longer to be found, the latter consist either of tracheæ alone, or of these and of delicate elongated cells accompanying them, the sieve-tube nature of which is no longer recognisable. Where and how the sieve-tubes cease and end has not hitherto been clearly made out in any case, and this point deserves more accurate investigation. The tracheæ always form the direct continuation of the xylem of the thicker bundles.

The ultimate *internal* ends and *anastomosing* branches of the bundles consist only of one or a few rows of short tracheides with fine spiral thickening, or reticulate thickening with narrow transverse meshes; their wall is often quite smooth in parts, appearing as if immature, e.g. in the leaf of species of Chamædorea, and Zea Mais (Fig. 175). Whether vascular perforations occur in these rows is at least doubtful, and not easy to decide.

The dilatation of the terminal branches above-mentioned comes about either by dilatation of the individual tracheides, or by increase in the number of rows. The end surfaces of the tracheides, bordering on the parenchyma, are usually cut off sharply, either transversely or obliquely. Characteristic differences corresponding to the several main forms of distribution of the bundles, or to the larger systematic divisions, are not to be observed, except that in general the thickness of the single terminal branches diminishes where the branches are numerous. Thus in the Ferns investigated, the relatively few final ramifications are comparatively thick, consisting of several rows, while in the foliage of Dicotyledons, where the reticulations are abundant and internal ends are present, the bundles are at last, as it were, broken up into single, or in places double tracheal rows, which end free with short branches (Figs. 172, 173). The transverse branchlets of most Monocotyledons consist of

FIG. 172.—Psoralea bituminosa (40). Ultimate ramifications of the bundles in a piece of a leaflet; at *r* is the edge of the latter.

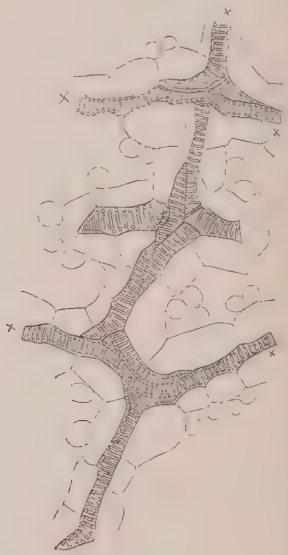

FIG. 173 (225).—Ultimate ramifications of vascular bundles from the leaf-lamina of Psoralea bituminosa; branched rows of tracheides, the ends marked × being torn off, the others terminating free. The whole branched row is surrounded by large cells containing chlorophyll; outside these are the circular transverse sections of some cells of the dense palisade parenchyma of the leaf.

one, or of quite a few rows of tracheal elements (Figs. 174, 175). The leaf of Welwitschia is to be mentioned as an exception to the rule, for its very numerous transverse branchlets (comp. Fig. 145, p. 303) have, so far as can be determined, the structure of complete vascular bundles provided with a multiseriate xylem and phloem, and it is only the short, thick, free-ending branches, springing partly from the angles of the cross-branchlets and partly direct from the longitudinal bundles, which consist exclusively of tracheides, the latter being inserted between the elements of the surrounding parenchyma.

As follows from what has been stated, the ultimate vascular branches often border directly on the parenchyma which in the laminæ of foliage-leaves contains

Chlorophyll. Its elements, in so far as they stand in immediate connection with the tracheæ, approach on the one hand the latter, on the other hand the typical parenchymatous cells in their form. This is the rule for the leaves of Monocotyledons and Dicotyledons; the exceptional case in which even the ultimate transverse branchlets are completely enclosed by stout sclerenchymatous sheaths occurs rarely in thick leaves of Monocotyledons, e. g. Rhapis, Vanda furva. In the leaves of Ferns the branches of the bundles are, so far as investigated, always ensheathed by one or a few layers of elongated cells destitute of chlorophyll[1], of which the outermost often has the structure of an endodermis up to the immediate neighbourhood of the free ends. At the free ends themselves the rows of tracheides pass over into the chlorophyll-parenchyma, through the intervention of some elongated smooth-walled cells.

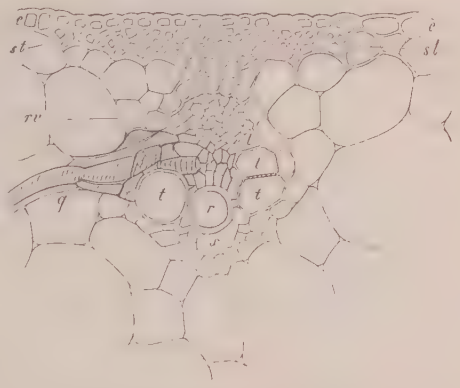

FIG. 174.—Zea Mais. Cross-section through a feeble (lower) leaf-sheath, about 2 cm. higher than Fig. 151, p. 331. *e* epidermis of the outer surface, bordering internally on a hypodermal bundle of sclerenchymatous fibres, *st*. On the inside of the latter one of the smaller longitudinal vascular bundles abuts; *r* annular vessel, *x* air-cavity, *t—t* pitted vessels; outside *t*, *r*, *t* are first narrow reticulated and pitted vessels (with a darker outline), then the phloem *rv*; *q* transverse branchlet springing from the tracheæ of the vascular bundle and consisting only of a few rows of tracheides.

In the case of many ends of bundles, which according to their local position must be called *peripheral*, no essential differences from the internal ends are to be mentioned. On the other hand, the structure shows peculiarities in those numerous cases, where the bundles run to parts of the epidermis described in Chap. I, which are distinguished by water-pores and water-filtration, by excretion of lime, or by glandular structure and secretion.

FIG. 175.—Cross-section through the lamina of the leaf of a young plant of Zea Mais. *o* epidermis of the upper, *u* of the lower surface; *h* hypodermal strands of sclerenchyma; *g*1 and *g*2 two small longitudinal vascular bundles in cross-section; *g*1 with three, *g*2 with two narrow vessels; both with a small phloem, consisting in *g*2 of only three elements; *g*3 transverse connecting branch between *g*1 and *g*2, consisting of a row of tracheides with partial fibrous thickening, and, like the two longitudinal bundles, enclosed directly in parenchyma containing chlorophyll.

Of the cases belonging to this series, in the first instance, the ends of the bundles in the furrows of Fern-leaves excreting water and lime (p. 106) are closely similar to the internal terminations in these leaves[2]. They show a knob-like swelling, in consequence of a sudden increase in the number and size of the tracheides, the latter being very short, with narrow

[1] Cf. Mettenius, Fil. hort. Lips. p. 9.

[2] Mettenius, *l. c.*

reticulations and pits, or with spiral fibres; one or two layers of delicate cells ensheath the whole end of the bundle, and separate it from the thin-walled epidermis of the furrow.

The ends of the bundles of the leaf-teeth of Drosera, and of the inner surface of the foliar pitchers of Nepenthes, are likewise placed close under specialised portions of the epidermis, and in point of structure stand next to those just described.

The leaf of species of *Drosera* (in particular of D. rotundifolia) has at its edge and on its entire upper surface numerous filiform teeth with broadened ends[1]. Those of the surface are, apart from differences of length, similar to one another; they are filiform processes, somewhat conically tapered, but swollen at the end to form an approximately ovate head. They consist of some layers of elongated cells, in the middle of which are one or rarely two narrow spiral vessels or rows of tracheides (I will not state definitely which) branching off from the net of bundles of the leaf-lamina, and having a straight course; the whole is covered by a single epidermal layer, the cells of which are likewise elongated. In the middle of the knob-shaped end the spiral vessel enters a group of closely-connected, short, reticulated and spiral tracheides, which has, as a whole, an ovate form, and constitutes the main bulk of the terminal portion. The layer of cells surrounding the vessels terminates below the middle of the group of tracheides, in the form represented in Fig. 176. At the point of transition to the head the epidermis first becomes short-celled, and then suddenly passes over into the three-layered covering of the surface of the knob, which, as Warming has shown, is derived partly from the primary epidermis, partly from the layer of meristem lying below the latter. The innermost layer of this covering forms a bell-shaped single stratum, consisting mostly of elongated cells, which is in immediate contact above and at the sides with the group of tracheides, while below, at the edge of the bell, it ends in the outer surface of the epidermis. The membranes of its cells are smooth and firm, similar in their reactions to those of an endodermis, the walls vertical to the surface being undulated. From the edge of the bell onwards the surface of the knob is covered by two layers of cells, which are thin-walled, and are distinguished in the fresh condition by their dense, intensely red contents. The inner of these two layers does not reach quite to the edge of the bell, and consists of small, isodiametric, polyhedral cells, which are very delicate, and are in uninterrupted connection one with another. It is everywhere covered by the outermost layer, which is continued immediately from the edge of the bell over the whole surface of the knob, and consists of polygonally prismatic cells in uninterrupted connection. The diameter of these cells vertical to the surface increases successively towards the apex of the knob; here it is about twice as long as the diameters coinciding with the surface, while at the base it is about equal to them. The delicate outer walls of these layers, which are covered later on with the sticky secretion (p. 101), show a very delicately undulated outline at the edges.—The teeth of the edge of the leaf are expanded at their ends to the form of a spatula or long

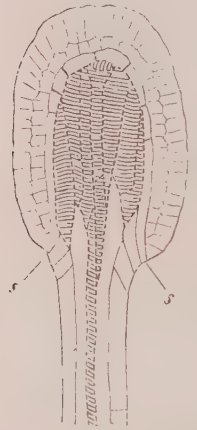

FIG. 176 (145).—Drosera rotundifolia. End of a tooth from the upper side of the leaf; axial longitudinal section. *s—s* the bell-shaped layer directly surrounding the end of the bundle; its lowest, very long cells, *s*, standing with their narrow outer wall in the epidermal surface, belong, as shown by Warming, and as their appearance indicates, to the primary epidermis; all the others, occurring above the apex, proceed from the subepidermal meristem. The same holds good of the cells of the second layer occurring above the apex: in so far as they border on the apical cells of the innermost layer they proceed from the sister-cells of the latter. Those, on the other hand, which belong to the lower edge of the knob, as well as the entire outermost layer, are derived from the primary epidermis.

[1] Compare Meyen, Secretionsorgane, p. 51.—Trécul, Ann. Sci. Nat. 4 sér. tom. III.—Nitschke, Botan. Zeitg. 1861, Nos. 22, 23, &c.—Martinet, Ann. Sci. Nat. 5 sér. tom. XIV.—Warming, *l. c.*; compare above, p. 57.—Darwin, Insectivorous Plants.

spoon, and have on the upper, somewhat concave surface of the latter the same three superficial layers as the middle teeth, while the edge and under-side consist of an ordinary one-layered epidermis. Under the three-layered portion of the surface lies a group of tracheides, corresponding to it in position, which are of the same structure as those of the middle teeth, and are connected with the network of bundles of the lamina by means usually of 2–3 spiral vessels.

On the inner surface of the pitcher of *Nepenthes* branches 1–2 vessels thick, coming obliquely from the network of bundles, end directly beneath the basal part of the digestive glands considered at p. 101, but by no means beneath all of them. Most of these organs, on the other hand, have no bundle-ends extending to them like those of other plants mentioned above.

Most bundles, which terminate beneath water-pores or glandular parts of the epidermis [1], consist of rows of tracheides, perhaps also of vessels, which run parallel towards the point of termination, diverging directly beneath the latter at greater or less angles, and then ending blind. The structure of the terminal elements is the same as in the internal ends; in species of Crassula reticulated tracheides with unusually large meshes occur. In all cases investigated, except Crassula, rows of delicate, smooth-walled cells, elongated in the same direction as the tracheæ, lie among the latter without any definite arrangement. These become more numerous

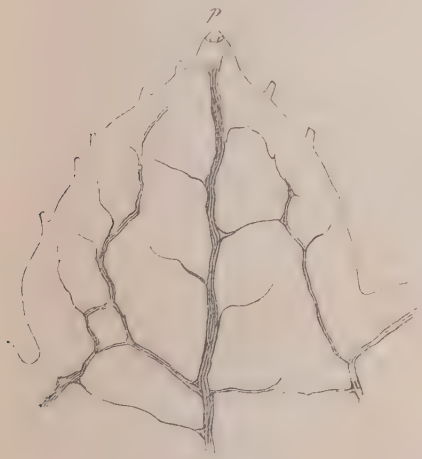

Fig. 177.

Fig. 178.

FIGS. 177, 178.—Primula sinensis. Fig. 177 (40). Outline of a tooth of the leaf with its branches of the bundles. The thickest of the latter ends below the water-pore *p*.—Fig. 178 (145). Longitudinal section vertical to the surface of the leaf, through the middle of a similar tooth. *o* upper, *u* lower surface of the leaf; *p* water-pore, below which is the air-cavity, and then the epithema, the cells of which are drawn somewhat too large. It contains a little chlorophyll throughout, and the bundle of tracheides, *g*, ends in contact with it. Under the epidermis on both sides is parenchyma containing abundant chlorophyll.

as the tracheæ between them terminate or diverge, and pass over gradually into a group of small delicate cells, which covers the ends of the vessels; these are in their turn immediately covered by the epidermis, and with reference to the former relation may be called the Cover, *Epithema* [2], of the end of the bundle. Either a single

[1] Compare p. 50, § 8, and p. 90. Most of the literature there cited refers also to the subject treated of here. [See also Gardiner, on the development of the water glands in Saxifraga crustata, Quart. Jour. Micr. Sci. July, 1881.]

[2] *ἐπίθημα*, the cover.

bundle ends in one group of epithema, or two or more converge, so as to end in a common group. The former, for example, is the case in the large leaf-teeth of Fuchsia, Primula sinensis (Figs. 177, 178), and Cucurbita, where the bundle-end is a thick, short strand, derived from the union of several convergent bundles inside the edge of the leaf; also beneath the furrows of the surfaces of the leaf of species of Crassula, in the glandular spots of the surfaces of the leaf of species of Malpighia, &c. The latter is the case in many teeth and crenations of the leaf, especially the broader ones, e.g. Brassica[1], Papaver, Tropæolum (Fig. 179), and many others. The arrangement of the parts is here such that one bundle coming from the middle of the leaf, and one or more marginal ones on each side, converge towards the epithema, and end at its circumference. Both cases, namely common and special epithemata, often occur side by side, e. g. in leaves of Crassula, in the marginal furrows of the leaf of Saxifraga Aizoon, elatior, and their allies (comp. Unger, *l.c.*)

FIG. 179.—Tropæolum majus (40). Course of the ends of the vascular bundles in a piece of the edge of the leaf at its median indentation. At *e* epithema, above which lie the water-pores figured at p. 52, fig. 19.

In the furrows or spots (mentioned in Sect. 8) of the surface of the leaf of certain species of Ficus, which have incorrectly been supposed to be without vascular bundle-terminations, in the glandular ends of the petiolar appendages of Passifloræ, Malpighiaceæ (e. g. Stigmaphyllum), and Amygdaleæ, and in the glandular prominences or depressions of Acacias, divergent rows of tracheæ with short articulations run into an epithema lying below the epidermis. These rows may belong, according to the particular case, to one or more bundles, or in several cases may equally well be considered as one bundle or as several.

In the furrows of the leaves of *Ficus*, according to investigations on F. neriifolia and diversifolia, a disc-shaped group of epithema lies below the epidermis, either over a knot of the network of vascular bundles, or over a single bundle; in the former case the vascular bundles meeting in the knot, break up, as it were, towards the side of the furrow, into numerous short rows of tracheides directed towards the latter; in the second case a bunch of tracheides branches off from the bundle and enters the epithema.

[1] Compare Unger, *l.c.* (above, p. 327), Taf. 2, fig. 17.

The glandular spots on the under side of the leaf of *Prunus* Laurocerasus also lie over a knot or a narrow mesh of the net of bundles, and from this some vessels or tracheides, which are not numerous, branch off into the epithema lying below the glandular epidermis.

In the petiole of *Passiflora cærulea* and its allies a bundle ending below the epithema enters the cylindrical appendages or teeth, which end with a concave glandular surface. The conditions are similar in the appendages of the petiole of *Amygdaleæ*. Several bundles running to the glandular terminal surface enter the broad round appendages of the petiole in *Stigmaphyllum*.

In the *Acacias* the glandular spots of the appendages of the petiole behave very differently according to the species (cf. p. 98). A number of small bundles, here and there reticulately connected, enter the elongated, wart-shaped projection of the base of the petiole of A. lophantha, running towards the free surface, and here ending in the epithema. Below the flat wart-like prominence on the upper edge of the base of the phyllodes of A. marginata, and A. calamifolia, numerous isolated short tracheæ branch off from the neighbouring strands of the net of bundles, and without being united into distinct bundles turn towards the epithema and there end. The same is to be seen here and there at the base of glandular pocket-like depressions of A. latifolia and its allies, but the vascular ramifications are here sparse and very short, while, on the other hand, the thick xylem groups of the bundle-net often border directly on the epithema.

As regards the characteristics of the group of epithema, in many cases it scarcely deserves a special name, as it is nothing but a small-celled parenchyma, which, on the one hand, passes over immediately into the other larger-celled parenchyma of the organ, and, on the other hand, into the interstitial cells of the end of the bundle. So, for example, in the glandular appendages of the petiole of the Passifloræ, and in most ends and teeth of leaves. Here the epithema is distinguished from the lacunar chlorophyll-parenchyma by the smaller size of its cells, and by their containing little or no chlorophyll, the places occupied by the epithema thus differing in their pale colour from the green surface of the leaf. The epithema passes over quite gradually on all sides into the large-celled chlorophyll-parenchyma; the water-pores of the epidermis lead immediately into the intercellular passages of the latter. In the leaf-teeth of Papaver orientale even all transitional forms are present between the small parenchymatous cells of the epithema and the tracheides of the bundle-ends. These epithemata have a very different form and extent, according to the shape and size of the bundle-ends and teeth of the leaf; in the narrow ends and teeth of the leaves of Fuchsia, Callitriche[1], and Primula sinensis, for example, they are quite small bodies, showing only a few cells in section, and lying immediately below the large stomatal cavity, which belongs to the water-pore, situated at the end. In the broad teeth of the leaf of Papaver and Brassica, and in the crenations of Tropæolum, the group of epithema, which receives several ends of bundles, is a many-layered small-celled parenchymatous mass, approaching 1^{mm} in breadth.

On the other hand, however, many ends of bundles run out into epithemata, which are sharply distinguished and limited. The furrows of the leaves of species of Ficus, Crassula, and Saxifraga, the glandular petiolar appendages of the Acacias, and many other cases, are examples of this. At the parts of the leaves indicated at p. 51, of species of Crassula, and of Rochea coccinea (Figs. 180–182), a thick bundle runs

[1] Borodin, *l.c.*; compare p. 51.

vertically to the surface under each epidermal furrow, ending some distance within the latter in a conical or hollow-conical expansion. Upon or in this expansion rests an epithema, of oval or elongated form according to the species, and extending to the epidermis, which contains water-pores. Its cells are on the average about one fifth the size of those of the surrounding chlorophyll-parenchyma, they are roundish or slightly elongated in the same direction as the vascular elements, with watery, colourless contents. They are almost uninterruptedly united with each other, and even the cavities below the water-stomata are small. In the furrows of the leaf of the Saxifrages mentioned above, the end of the vascular bundle is expanded into a large epithema of an approximately conical form, with its base resting on the epidermis of the furrow. Its structure is very similar to that of Crassula, its cells are elongated in the same direction as the tracheæ, and the whole body, like the vascular bundles themselves, is ensheathed by a layer of cells which are very rich in tannin. The epithemata in

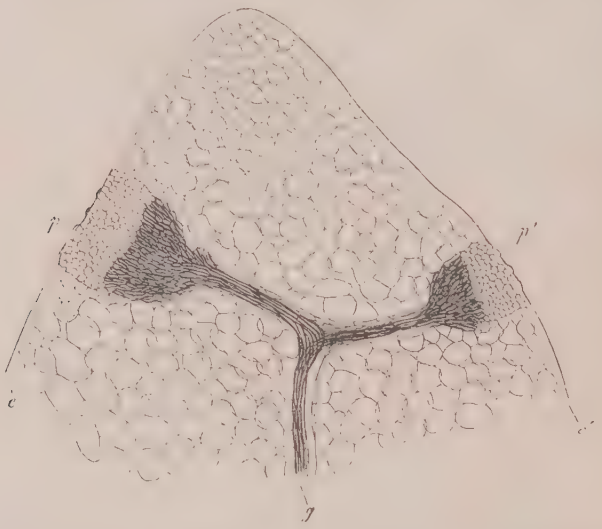

FIG. 180.—Crassula arborescens. Longitudinal section, vertical to the leaf-surface, through the apex of a leaf. Magnified 30—40. *e—e'* epidermis; *g* vascular bundle, divided into two branches, which terminate below a small-celled epithema in broadly conical ends consisting of short tracheides; the branch at *p* on the upper, that at *p'* on the lower surface of the leaf.

the furrows of Ficus have an approximately discoid general form, are round-celled, and in other respects are also similar in structure to those of Crassula. The same also holds good in general of those epithemata which lie below the glandular portions of the epidermis. How far the nature of the contents of their cells shows remarkable peculiarities, still remains to be more exactly investigated.

SECT. 112. In the leaves of the *Coniferæ*, as stated above, the finer ramifications of the bundles are absent; the leaves are traversed either by a number of bundles of approximately equal thickness, or in most cases by a single median one; in most Abietineæ by a median pair of bundles running close side by side, only separated from one another by one or two layers of elongated cells (e. g. Abies excelsa, pectinata, Pinsapo; Cedrus Libani; Pinus Pinaster, Laricio), or by a thick strand of sclerenchymatous fibres. The bundles are collateral, and their orientation is

normal. Towards the end they are tapered, and the xylem and phloem diminish in such a manner, that here also the ultimate termination consists only of one or a few rows of short tracheides. They are distinguished by the fact that within the lamina of the leaf, as if to replace the finer branches, the edge of the xylem is expanded throughout its entire length into a border, consisting of rows of short tracheides inserted in the parenchyma of the leaf. This fringe of tracheides, which was first accurately described by Frank in the case of Taxus[1], and afterwards more generally demonstrated by Mohl[2], is absent, or at least extremely feeble, in Larix europæa alone of forms known to me: it arises, in the case of the Abietineæ, exclusively from the outer, remote edges of the pair of bundles, in the other cases investigated from both sides of each of them.

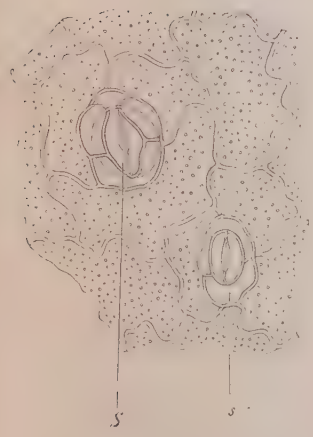

Fig. 181.

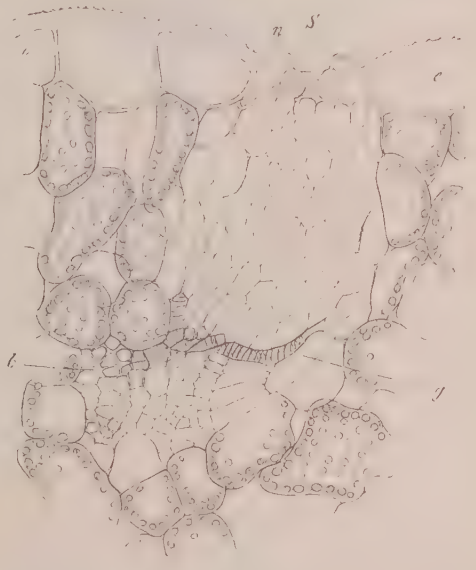

Fig. 182.

FIGS. 181, 182.—Rochea coccinea (200). Fig. 181. Fragment of the epidermis from the edge of the leaf. *S* water stoma; *s* air stoma, with subsidiary cells. The scattered dots are wart-shaped projections of the outer walls.—Fig. 182. Section through the edge of the leaf vertical to the surface. *e*—*e* epidermis, *S* water stoma, *n* subsidiary cell, *b* somewhat thick vascular bundle in cross-section. The meshes with thicker and double outlines are the sections of bundles of tracheæ which run to neighbouring bundles; the more delicate outlines are those of the accompanying elements. A short strand goes off from *b* and runs towards *S*; the tracheides of which it consists diverge and embrace the delicate-celled group of epithema lying between *b*, *g*, and *S*. All round is large-celled chlorophyll-parenchyma.

It is attached to the xylem by means of one or two longitudinal rows of tracheides, more or less frequently interrupted by parenchymatous cells, and from here projects on each side into the surrounding parenchyma; in most of the species it has the form of a plate, which is either plane or a little curved, and approximately follows the direction of the leaf-surfaces (Taxus, Cephalotaxus, Torreya, Taxodium sempervirens, Cunninghamia (Fig. 183), Juniperus (Fig. 184), Thuja, Thujopsis, Gingko), or is curved from each side round the body of the vascular bundle, and is separated from the latter and from the plate on the other side only by a few rows of parenchymatous

[1] Botan. Zeitg. 1864, p. 167, Taf. IV.

[2] Ibid. 1871, p. 10. Mohl calls the tracheide-border *Transfusion-tissue*. [See also Zimmermann, über das Transfusions-Gewebe, Flora, 1880, p. 2.]

cells. The border is in fact curved round the xylem in Sciadopitys, Araucaria brasiliensis, Cryptomeria, and Dammara; round the phloem in Abies pectinata and Pinsapo. In Abies excelsa and the Pines (P. silvestris, Laricio) it is split as it were into two plates on each side at its place of attachment, which, in a manner still to be more accurately described, are bent, the one round the xylem, the other round the phloem, so that the pair of bundles is completely surrounded by the border of tracheides.

The plates of tracheides are in many cases, especially in Podocarpus Meyeriana Endl., of nearly equal thickness throughout in every cross-section; in the other

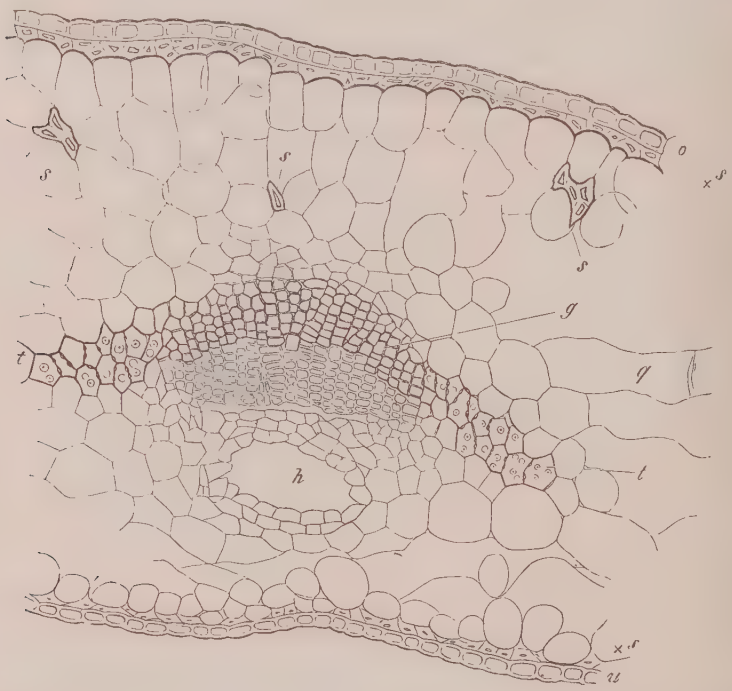

FIG. 183.—Cunninghamia sinensis. Cross section through the leaf (220). *u* lower, *o* upper surface; *h* resin passage; *x s* sclerenchymatous fibres of the hypoderma, *s* those scattered in the parenchyma; *g* xylem of the median bundle; *t* tracheide border of the latter. Below, towards the resin-passage, is the thin-walled phloem; the white band at its boundary towards the parenchyma surrounding the resin passage is the compressed primordial tissue of the phloem; *g* transversely elongated parenchymatous cell of the middle of the leaf.

cases mentioned, except Abies excelsa and the Pines, they are thicker on their outer edge, i. e. that remote from the vascular bundle, than on the inner attached edge, in consequence of increase in the width and number of layers of their elements; this often takes place to such an extent that the cross-section becomes wedge-shaped, e. g. Taxus and Podocarpus Thunbergii.

The tracheides of the border are in general arranged in fairly regular rows both in the direction of the length and of the breadth of the leaf; these rows often show interruptions, which are filled up by parenchymatous cells, but all are at some points in immediate connection with one another. At the inner edge, which is attached to the xylem of the bundle, their form is similar to that of the tracheides of the latter,

namely elongated; but they are on the average shorter and wider, and have terminal surfaces, which are but little oblique, and may even be horizontal. As their distance from the inner edge increases, their length rapidly diminishes, while their width increases, so that in the outer part of the border they are not longer, and are often even shorter than they are broad, being similar in form and size to the neighbouring parenchymatous cells.

These conditions appear in a special form in Podocarpus Meyeriana, Thuja gigantea, and in the Pines and Abies excelsa. In the two first-named the border is very broad, it projects deeply into the middle of each half of the leaf in the form of a flat wing. Its tracheides, with the exception of the innermost, are, with reference to the diameter of the leaf, much broader than long, thus having their greatest diameter directed towards the edge of the leaf; they form rows running towards the latter,

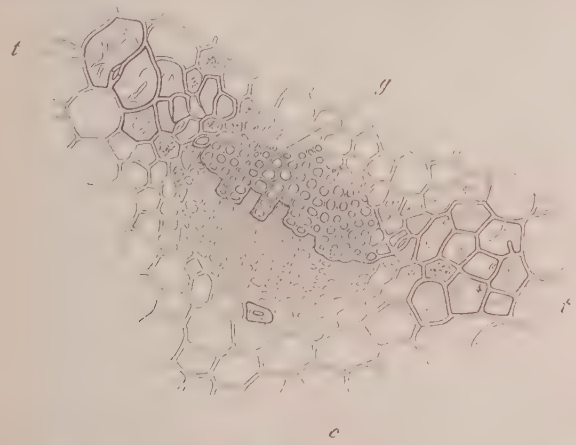

FIG. 184.—Juniperus communis (225). Median vascular bundle of the leaf. *g* xylem; *c* isolated sclerenchymatous fibres at the outer border of the phloem; *t* border, consisting of tracheides with bordered pits and cross beams. The parenchymatous cells occurring near or between the latter are dotted in a granular manner.

which are often interrupted, but are in contact with one another, and might be termed a narrow-meshed net of uniseriate vascular bundle terminations.

In the connate sheathing-base of the flat pair of leaves of Thuja gigantea, the border of tracheides of each leaf is expanded into a low wing, which runs to meet that of the opposite leaf, and unites with it to form a transverse girdle.

In the Abietineæ last-mentioned[1], the pair of vascular bundles lies in an approximately cylindrical central portion of the leaf, which is free from chlorophyll, and is separated from the surrounding chlorophyll-parenchyma by a parenchymatous sheath with somewhat stouter walls (cf. Fig. 185).

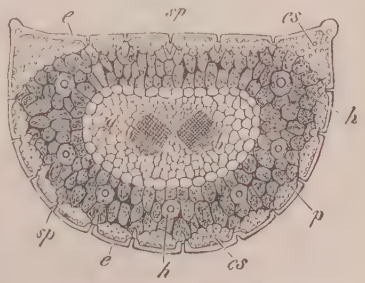

FIG. 185.—Cross-section through the leaf of Pinus Pinaster (50). *e* epidermis, *es* hypodermal strands of sclerenchymatous fibres, *h* resin canals, *p* chlorophyll-parenchyma; *g—b* colourless tissue of the middle of the leaf, containing the two vascular bundles. From Sachs' Textbook.

[1] See Hartig, Naturgesch. d. forstl. Culturpflanzen.

Throughout the entire central portion are distributed rows of tracheides, which in all directions are alternately in connection with one another, and interrupted by rows of parenchyma, or by isolated sclerenchymatous fibres; they are connected with the edge of the vascular bundle in the manner described above.

In the Abietineæ last-mentioned the breadth and thickness of the border of tracheides cannot be more exactly defined than by the statement, that the colourless central portion of the leaf is 2–5 layers of cells thick all round the pair of vascular bundles. In the other cases, where it is more sharply limited, its breadth may be stated as on the average equal to that of the vascular bundle, the number of rows of tracheides in the direction of its breadth being about 5–8. In the direction of thickness, vertical to the latter, the number of rows in the thickest external part is usually on the average 4–5, more rarely, when the border is broader, only 1–2 (Cunninghamia, Cedrus, Juniperus communis). In Gingko and Prumnopitys the border is quite feeble, showing only 1–3 tracheides in cross-section. On the other hand, in Podocarpus Meyeriana, so often referred to, it is 1–2 layers thick, but on the average 15 rows broad, while in the above-mentioned transverse wing of the sheathing base of the leaf of Thuja gigantea it is 25–30 rows broad. At the end of the bundle the short-celled external edge of the border passes over directly into the short tracheides which form the ending of the bundle itself.

The structure of the tracheides themselves is in general that given in Chap. IV, for this form of tissue. In the living leaf I always found them to contain water, not air. Their lignified walls agree generally in structure with those of the spindle-shaped tracheides which form the edge and the external region of the adjoining xylem, and in structure are identical with or similar to those of the secondary wood of the same species. In most cases they have the large round bordered pits universally distributed among the Coniferæ (cf. Fig. 183). In many forms, on the other hand, they are smooth and thin, as in Abietineæ, species of Cunninghamia and Thuja, often also in Araucaria imbricata and brasiliensis, and in Sciadopitys. Many tracheides in the three species last-mentioned, and all of them in Taxus, Dammara, Gingko, and species of Podocarpus, have reticulated and spiral thickening in addition to more or less numerous often isolated bordered pits, in varying distribution, which for most species requires to be more accurately ascertained. In the leaves of the species of Juniperus investigated (J. communis, Oxycedrus, oblonga, macrocarpa, Mohl, *l. c.*, also J. sabina) the tracheides of the border are distinguished by the transverse bars described at p. 163, in Biota orientalis by the projecting pegs mentioned at p. 164 (Fig. 184).

The reticulated elements at the circumference of the vascular bundles of the leaf of Welwitschia, represented at p. 335, Fig. 157, must be reckoned among the borders of tracheides in question, so far as the dead material admits of a decision. They are usually quadrilaterally prismatic, short, almost cubical, while some are elongated and even have tapered ends. Their structure is that of tracheides with a narrow-meshed, reticulated membrane, and with isolated bordered pits between the threads. They are arranged in longitudinal rows, which follow the vascular bundle, and are often irregularly interrupted by parenchyma, but at many points stand laterally in direct connection both with each other, and also with the xylem of the bundle; the latter is the case both at the sides of the longitudinal bundles,

and more especially at the free ends of the transverse branchlets (cf. Fig. 145, p. 303).

Sect. 113. In typical *roots*, it is simply the meristematic group of the growing point which forms the end of the vascular bundle.

Those parts of *Phanerogamic Parasites* which are developed inside the host, (intramatrically), as well as their *haustoria*, behave differently. According to the existing investigations, for the details of which the special works are to be compared[1], these organs are traversed by vascular strands, which are quite similar in structure to the ends of bundles in the foliar expansions; they form strands of vessels with short elements, usually reticulated or pitted, accompanied by rows of moderately elongated thin-walled cells, with acute ends; or they are isolated vessels with very short, and then usually very irregular elements, traversing the parenchyma, and often actually interrupted by parenchyma, thus constituting isolated portions of vessels, or tracheides, enclosed in the latter. These strands are, on the one hand, connected with the xylem of the bundles of the extramatrical organs of the parasites; on the other hand, they extend at definite points to the limiting surface between the intramatrical tissue of the parasite and the tissue of the host, here entering into close connection with the latter, and in fact becoming as a rule closely attached to the equivalent tissue, i. e. to the vessels and woody elements of the host. The intimacy of the connection may go so far that it becomes difficult to determine the boundary where the vessel of the parasite begins, and that of the host terminates. Sieve-tubes have not been found in company with these vessels and strands of vessels.

The following may be mentioned as examples, reference being made to the numerous individual forms described in the special works.

(1) The haustoria of the Cuscutas, Cassythæ, Rhinanthaceæ, and Santalaceæ. In the first two groups they arise from the twining stem, and penetrate the stem and foliar organs of the host, round which it is twisted. In the two families last-mentioned they arise on the roots, penetrating the roots of the host. In most cases they have the general form of conical warts, with the base adhering firmly to the host, and from the middle of the attached surface an approximately cylindrical or flat peg, the *sucker*, penetrates the tissue of the host. In the haustorium an axial, broad, small-celled strand of parenchyma, the *core*, is to be distinguished from a large-celled *cortex*; the core is continued directly into the sucker. In Cuscuta the extramatrical portion is very little developed, the haustorium may be said to consist only of the swollen sucker, which springs from the surface of the stem adhering to the host. Vascular strands branch off from the xylem-groups of the bundles of the main axis, so as to pass through the core usually until they reach the inner surface of the sucker where it meets the vascular bundles or the wood of the host. In the normally developed haustoria of Thesium, Santalum, and Osyris there are two thick flat strands, which first diverge, with a curved course at the periphery of the flask-shaped core, and converge again in the sucker; in Cuscuta, Cassytha, and the Rhinanthaceæ there is an axial strand, usually penetrating to the wedged-in end of

[1] Graf zu Solms-Laubach, Bau und Entwickelung der Ernährungsorgane parasitischer Phanerogamen; Pringsheim's Jahrb. Bd. VI.—Id. Das Haustorium der Loranthaceen, &c., Halle, 1875.—L. Koch, Entw. d. Cuscuten, in Hanstein's Botan. Abhandl. Bd. II. Heft 3.

the sucker. The vessels of the strands consist, in all these haustoria, of short elements communicating by wide perforations; in the sucker they are usually more elongated, the reticulate thickenings of their membranes being often imperfectly developed at the surface of the process.

(2) The intramatrical ramifications of the haustorium of Viscum and Phoradendron, which have been described as cortical roots, are traversed by an irregular axial vascular strand, which ends in the apical meristem, and is developed slowly and relatively late. In the 'borers,' which, starting from the cortical root, penetrate the wood of the host, like wedges, the middle is occupied by a relatively thick mass of vessels, the remainder of the body consisting of large-celled parenchyma. The vessels do not reach the edge of the borer.

In the broader outer portion, the bundle is irregularly branched, and from the branches numerous vessels with short elements run generally with a curved course towards the lateral surfaces of the borer, and here attach themselves to the elements of the wood of the host. In very old borers, which have finished their growth, the vessels are continuous with those of the cortical root. So long, however, as the borer is still growing, they are separated by a zone of meristem, which carries on the growth, and lies in the cambium of the wood of the host (Chap. XIV). The vascular body of the borer may be massively developed, while as yet no vessels have been fully formed at its point of origin in the cortical root. Arceuthobium Oxycedri, which is much smaller in all its parts, has no vessels at all in the smaller branches of its cortical roots, or in its small 'narrow' borers; the latter simply consist of a few rows of large parenchymatous cells. The thicker cortical roots and borers are similar in structure to those of Viscum album, but are simpler, as corresponds to their small bulk. Similar conditions to those in Arceuthobium recur in the intramatrical thallus of Pilostyles, with specific variations.

(3) The flat intramatrical body of *Cytinus* Hypocistis (cf. Graf Solms, *l.c.*, Taf. 36, 37), which is irregularly discoid, and on its lower surface wedged with irregular protrusions into the wood of the host, is traversed throughout by isolated, very irregular vessels, which are abundantly branched and reticulately connected, and which in the wedged protrusions are attached to the ligneous elements of the host. The elements of the vessels are as a rule irregularly rounded, with a reticulated wall, and are in communication by means of large round holes.

(4) In the tuberous regions of attachment of the *Orobanches*, the vascular bundles, both of the parasite and of the host-root bearing it, are as it were broken up into a loose web of numerous vessels with short elements, those of the parasite standing in immediate continuity with those of the host. A sharp boundary, whether between the vessels or between the parenchyma of host and parasite, is often only to be recognised in the youngest stages[1].

In the tuberous regions of attachment of most genera of Balanophoreæ (Helosis, Lophophytum, Scybalium[2]), the conditions of structure are similar to those in Orobanche, except that the vessels are clearly distinguishable from those of the wood of the host-root, as far as the point of attachment to the latter. Essentially the same holds good of the Rafflesiaceæ.

[1] Caspary, Flora, 1854, Taf. III.

[2] Eichler, Balanophoræ brasilienses, *l.c.* (p. 254).

(5) In the regions of attachment of Balanophora and Langsdorffia, according to the authors mentioned, and the earlier investigations of Göppert[1], an additional phenomenon occurs, which likewise belongs to this series. In these cases thick, variously ramified vascular bundles, arising as branches from the wood of the host-root attacked, grow into the parenchyma of the tuber of attachment, their branches having broad blind ends in the parenchyma of the tuber. According to the existing investigations, a direct connection between these excrescences and the parasites' own bundles does not take place, or is at any rate doubtful. The bundles of the excrescence are thick strands attaining more than 1^{mm} in thickness, and their branches have broad ends, which may even be swollen in a club-like manner. They consist of thick vascular masses, which are accompanied by delicate elongated elements requiring further investigation; they are penetrated by narrow divaricating bands of the thin-walled parenchyma belonging to the parasite (cf. Graf Solms, *l. c.*).

Sect. 114. *Connections of Bundles.* Where one vascular bundle-trunk branches off from another, or, otherwise expressed, where it attaches itself to another, the equivalent regions and elements of the two are in continuity. Where the arrangement and orientation of the parts of the bundles in question are similar, as is the case in most stems, and in the lamina of foliar expansions, the above fact indicates the structure of the region of union in the most essential points; various individual differences follow from the general principle that the special structure of every bundle may change in successive transverse sections.

Where the arrangement of the parts and the orientation of the bundles is different, torsions and displacements, both of the individual portions of the bundle, and of any strands or sheaths that may accompany it, must take place towards and at the place of union, in order to establish continuity of the equivalent elements; and with these torsions other changes of structure may be connected, besides those relating to the orientation of the parts.

Those cases of the union of bundles of unlike orientation which are remarkable in these respects fall under two main categories, namely, connections between bundles belonging to the same axis, and connections between the bundles of a main and a lateral axis.

I. Of the former category we have here first to mention the connection of the bundle-system of the stem with the radial bundle of the main root in the typical Dicotyledons and Gymnosperms[2]. The hypocotyledonary stem of these plants contains, as described above, two or more separate, collateral bundles of normal orientation, and towards the main root these approach one another so as to unite to form its axial bundle. In the hypocotyledonary stem the primitive tracheæ lie at the inner edge, the phloem at the periphery of each bundle. In the axial bundle of the root the primitive vessels occupy the outer edge of every xylem-plate, and the phloem-bands alternate laterally with the xylem-bands. The investigation of the longitudinal

[1] *l. c.* at p. 254.

[2] Mettenius, Anat. d. Cycadeen, *l. c.* p. 602.—Dodel, Der Uebergang des Dicotyledonen-Stengels in die Pfahlwurzel, Pringsheim's Jahrb. Bd. VIII.—Strasburger, Die Coniferen und die Gnetaceen, p. 360.—Van Tieghem, Canaux Sécréteurs, *l. c.*—S. Goldsmith, 'Beitr. zur Entwickelungsgeschichte d. Fibrovasalmassen im Stengel und in der Hauptwurzel der Dicotyledonen,' could not be made use of for the present work. [Gérard, Recherches sur le passage de la racine à la tige, Ann. Sci. Nat. 6 sér. tom. 11. 1881.]

course of the bundle shows that the primitive vessels extend continuously from the bundles of the stem into that of the root, and thus gradually become displaced, on their way to the root, from the central into the peripheral position. This is accompanied by a corresponding gradual displacement of the other parts of the bundle, in such a direction that, on their union to form the root-bundle, the radial structure of the latter is also attained. Together with these displacements, division and re-union and disappearance of certain parts of the bundle may successively take place. It is obvious that a variety of particular cases are possible according to the different number of the bundles in the hypocotyledonary stem, and of the rays in the bundle of the root.

Among the particular cases which have been more accurately investigated, that described by Strasburger in the case of *Biota* orientalis, which presumably often recurs elsewhere, is especially simple and intelligible. The hypocotyledonary stem contains in its upper part two bundles descending perpendicularly from the two cotyledons; the bundle of the main root is diametrally diarch. In each of the cotyledonary bundles as they gradually approach each other a radial division of the phloem into two halves begins. Further below the two halves become more and more distant, and are shifted into the same tangential plane with the xylems; each then approaches that coming from the same side of the other bundle and unites with the latter to form one broad phloem-group. The xylem-groups of both bundles go through the above-mentioned displacement or torsion in the same part of their course; the two broad phloem-groups therefore alternate with the xylem-plates of the root-bundle, which have their primitive vessels directed towards the outside.

In the *Abietineæ* with many cotyledonary bundles and a polyarch bundle in the main root (cf. p. 356), as many cotyledonary bundles as the bundle of the root has xylem-plates undergo torsion during their downward course through the hypocotyledonary stem; their phloem-groups shift laterally into the space between the xylem-groups, the primitive vessels of the latter shift from the central to the peripheral edge. The xylem-groups of the remaining cotyledonary bundles gradually disappear, while the phloem-groups amalgamate with those which undergo the deviation described.

In *Phaseolus* four decussate pairs of bundles traverse, in the simplest case, the hypocotyledonary stem. The xylem-groups of the eight bundles are separate, the phloem-groups are united to form four broad curved bands, which together form a ring only interrupted between the two bundles of each pair. The xylem-groups of the bundles leave the cotyledons with normal orientation, but then go on changing their direction in such a manner that the primitive vessels of each come to stand in one tangential row with the others; and in fact the bundles of each pair here turn their primitive vessels towards each other. At the boundary of the main root the xylem-groups of each pair revolve round the primitive vessels in such a manner that the latter come to lie outside, the remaining vessels towards the inside; the further down, the more acute is the angle which the bundles of a pair form with one another, until they finally become parallel, and fuse to form one of the four xylem-plates of the root-bundle. The phloem-strands alternating with the latter are the direct continuation of the four broad bands of the hypocotyledonary stem. Both in the latter and in the root they are each supported externally by a thick strand of sclerenchymatous fibres, which however is interrupted for a short distance at the point of transition to the root. In other less simple cases, additional intermediate pairs of bundles lie between the above-mentioned four pairs of bundles of the hypocotyledonary stem. These usually end blind at the lower boundary of the stem; one of them however frequently enters the root, so as to form a fifth xylem-plate of the pentarch root-bundle in the same way as the four main pairs.

2. The united portions of the bundles in the stem of certain Aroids and Pandaneæ (p. 268) are distinguished by a distribution and orientation of their

elements, with reference to which van Tieghem[1] has appropriately termed them compound bundles. The bundles, which on their downward course from the leaves are at first collateral with normal orientation, usually unite to form a body of round or irregular cross-section, their phloem-groups uniting either directly or by means of an intermediate bundle of sclerenchyma to form a joint strand, at the periphery of which lie the xylem-groups, which towards different sides are sometimes separate and sometimes fused. The number and structure of the latter and the configuration of the whole bundle change, both in successive cross-sections of the same individual and in the different species. For details, van Tieghem, *l.c.*, is to be consulted.

Similar, less conspicuous phenomena no doubt occur here and there in other stems of Monocotyledons, and in stems and petioles with medullary bundles.

II. The following rules, which are to be stated with reference to Sect. 108, and to the developmental data given below in Sect. 117, hold good for monopodially branched *roots* with regard to the attachment of the vascular bundles of lateral branches to that of the main axis.

Apart from a few exceptions to be mentioned below, every lateral root arises on the outside of the vascular bundle of its relative main root, in front of the centre of the outer edge of a xylem-plate. Accordingly, in the case of diarch and many polyarch roots, their xylem-plates are attached to the corresponding outer edge of the bundle of the main root, their phloem-strands to those alternating with it.

In the polyarch bundles of many Monocotyledons, the xylem-plates are attached not only to the corresponding plates of the main root, but also to the two neighbouring lateral ones, while the phloem-bands are attached to those bands in the main root which alternate with the three xylem-plates mentioned; van Tieghem found this to be the case, for example, in the ramifications of the adventitious roots of Iris Germanica, Asphodelus ramosus, and Asparagus. The division of the lateral bundles, in the case of Pandanus and the Palms, into branches which penetrate further and deeper, was mentioned above at p. 316. In the Grasses, on anatomical grounds, which have still to be explained below, Sect. 117, the lateral roots do not stand in front of the xylem-plates, but in front of the centre of the phloem-strands of the bundle of the main root; accordingly their xylem-plates are attached to the two next lateral plates of the main-root, their phloem-groups to the corresponding ones of the latter. A similar relation obtains, for similar reasons, among the Pittosporeæ. As will also be further explained in Sect. 117, each lateral root in the Umbelliferæ and Araliaceæ is placed between a xylem and phloem-group of the main root; its xylem is accordingly obliquely attached to that surface of the corresponding plate of the main root which faces it[2]. The same position of the lateral roots and insertion of their bundles occurs, according to van Tieghem[3], in Lycopersicum, while nearly related plants, e. g. Solanum tuberosum, show the usual behaviour of oligarch roots mentioned above.

In the case of the other connections of bundles between main and lateral axes, nothing essential need be added to what has been said in earlier paragraphs, and at the beginning of this, respecting the orientation of the parts of the bundle.

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[1] Structure des Aroidées, *l.c.*

[2] Van Tieghem, Symmétrie de Structure, *l.c.*

[3] *l.c.* 226; cf. also § 117.

As regards the special structure, the general rule holds good, that at the points of attachment of lateral organs on stems and roots the elements of the vascular bundle are short in comparison with those of the main bundles, because they in some cases arise at such places as never undergo more than a slight elongation, and in others attain their development after the elongation of that portion of the main axis which bears them is far advanced. This phenomenon is especially familiar in the case of the nodes of vascular plants; it appears the more conspicuously the more abundant the subdivision and ramification of the bundles where they are attached (comp. Sects. 94, 95). The lateral walls of the short joints of vessels or of tracheides in these regions are in the very great majority of cases pitted, or reticulately thickened, and in the latter case they usually have low, transversely elongated meshes. Spiral and annular threads seldom occur, and then usually pass over within a short distance into cross-meshed reticulate thickening, e. g. in the node of many Commelineæ. The tracheal elements of one bundle as a rule attach themselves to the equivalent elements of another with tapered, acute ends, which adhere for some distance to the lateral wall of the other; the attached ends are rarely cut off transversely.

The attachment of the sieve-tubes to one another appears to take place in a similar manner to that of the vessels, especially according to isolated observations on the Cucurbitaceæ. More accurate investigations on this point do not however exist.

C. DEVELOPMENT.

Sect. 115. The vascular bundle is formed from a strand of meristematic cells, which, in accordance with the definitive form of the bundle-elements, assume a form elongated in the longitudinal direction of the bundle, and undergo divisions in the same direction excepting where they give rise to the shorter parenchymatous cells belonging to the bundle. These initial strands of the bundles are therefore distinguished, in a degree corresponding to the progress of histological differentiation, from the surrounding non-equivalent tissue, and especially from the initial layers of those masses of parenchyma which continue short-celled owing to persistent transverse divisions. To this is further added the usually smaller growth of the elements of the bundle in a transverse direction, as compared with the short-celled surrounding tissue; the initial strand has narrower cells than the surrounding tissue. Essentially the same phenomenon appears when other strands consisting of elongated elements, especially for example strands of sclerenchymatous fibres, become differentiated out of the primary meristem, and from tissue which remains short-celled, whatever may be the anatomical definition of the region in which they arise. Therefore where a fibrous-strand immediately accompanies a vascular bundle, it is not to be distinguished from the latter in the initial stage, or at least not sharply.

The long-celled initial strands of the vascular bundles, and in certain cases the fibrous tissue accompanying them, were called by Nägeli[1] Cambium-strands, in partial agreement with the older terminology, the term Cambium being used for the long-celled initial strands, as distinguished from the short-celled 'Meristem.'

[1] Beitr. I. p. 2. Compare the footnote at p. 4.

Sachs[1] has introduced the name Procambium for the former, because the term cambium, if applied to them, would be ambiguous, meaning two different things, namely, on the one hand the strands in question, and on the other the initial layer of secondary growth, which has been traditionally designated by this name, and of which Chap. XIV will treat. We here entirely pass over the use of the word cambium mentioned at p. 4, introduced by some authors for all those groups of cells which are called Meristem in this book. Finally, Russow[2] call the strands in question Desmogen.

It is essentially a matter of indifference which name is used, provided it be known what it means; that is, in the present case, that we are dealing with groups of cells which fall under that general conception of Meristem—gradually passing over into differentiated tissue—to which we have adhered in this book, and that we are dealing with strands which are different from the cambium to be treated of in Chap. XIV, although they may actually stand in the closest anatomical and genetic relation with it. It may well be advisable, however, to avoid any term which would recall a different idea, or which would seem to imply more than the simple fact that the strands in question are the young vascular bundles, i. e. the beginnings of the latter; and for this reason we may apply to them the term initial strands or initial bundles, in agreement with the other terminology used in this book. The initial strands arise from and consist of initial cells, of successively different degree and value, from which the elements of the vascular bundle are derived.

In typical *roots* the axial meristematic strand, termed the plerome in the Introduction, is the initial strand for the vascular bundle. Its differentiation from the surrounding meristematic layers, the degree of completeness of which differs according to the particular types, has been described above in the Introduction; in the case of lateral roots arising on a main root, this will still have to be discussed below. Here we have only to repeat that the individual parts of the vascular bundle are already at an early stage to be distinguished as special layers of the initial strand. In Fig. 186, reproduced here, and in Figs. 2 and 4–6, above, the layer or row marked *p* and *pc*, the same which in Fig. 3 is marked *f* next to $x-x$, is the pericambial layer, which may be followed up to the common initial cells lying at the apex of the plerome body; in the same figures *v* or *g* marks in each case an initial row for a vessel or row of tracheides, and of this initial row the same holds good as of the pericambium. In the case of the root-bundle of the Ferns and Azollas, similar conditions to those in the Phanerogams may be demonstrated with still greater sharpness, as shown by Nägeli, Leitgeb, and Strasburger.

In *stems with a simple axial bundle* the primary plerome body, like that in the root, has the significance of an initial strand (Fig. 1, p. 8).

In *stems with a complex bundle-system*, and in *leaves*, the conditions are different. We will first consider simply the earliest appearance of the vascular bundle, without reference to the question as to its special place of origin. The development begins with the fact that a single row, or more frequently a strand consisting of several rows, of the originally uniform primary meristematic cells, lying in a position corresponding to the course of the bundle, undergoes divisions by means of longitudinal walls,

[1] Textbook, 2nd Eng. ed. p. 110.

[2] Vergl. Unters. p. 178.

while growth in the transverse direction is relatively slight. These divisions are repeated with a frequency varying according to the particular case. In thick, and especially in collateral bundles, they often still go on for a long time on the boundary between phloem and xylem, when at the edges of the bundle the differentiation of the tissues is already completed. In this case the later-formed septa in the border-zone just mentioned assume the tangential direction spoken of above (p. 325); the earlier stages of division always take place in all directions successively.

The completion of the definitive elements of the bundle begins in each transverse section with those of them which have been described above as the primitive elements, and thus in the regions occupied by the latter. It spreads centrifugally from each of these over the cross-section, when they are situated in the interior of the strand. If they occupy one edge of the strand the development in general proceeds towards the opposite edge; in radial bundles, as described above, it goes on in the centripetal direction; in collateral bundles it is centripetal in the phloem and centrifugal in the xylem; in concentric bundles, and in the special case of leaves of Cycads described above at p. 336, the development goes on in different directions according to the number and position of the primitive groups, the direction being generally determined by the rule first stated. Where the edge of the phloem is broad the development extends along it from the first points of development in the same order. The development always begins with that of the first primitive elements of the phloem, Russow's protophloem; the primitive elements of the xylem appear later in course of development. Where a bundle is accompanied by sclerenchymatous fibres the development of the latter takes place later, often much later, than that of the two primitive groups, and independently of their appearance.

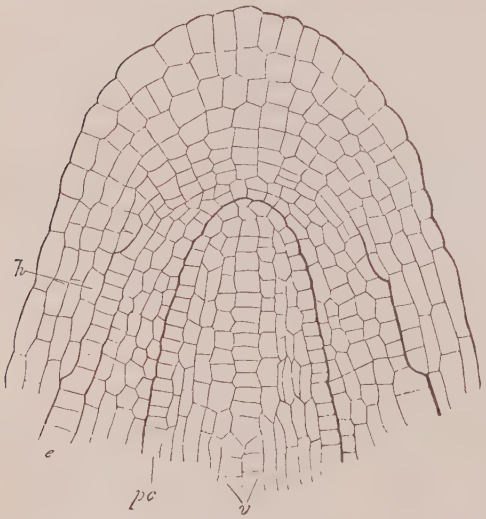

FIG. 186 (210).—Polygonum Fagopyrum. Root-apex, median longitudinal section. *pc* pericambium, outside boundary of the plerome strand; *v* rudiment of a vessel; *e* dermatogen or epidermis; between *pc* and *e* periblem; *h* root-cap.

With reference to the longitudinal course of the bundle, both the definitive completion and the first origination may proceed in the acropetal, or conversely in the basipetal direction[1]. It is further at least conceivable that in the same bundle the progression of the two processes may take place in unlike directions, or even that each of them goes on in a different direction at different parts of the course of the bundle. Sanio's statement[2] that, according to his investigations, carried out in the

[1] [Compare Trécul, Ann. Sci. Nat. 6 sér. tom. XII. p. 251, 1881.] [2] Botan. Zeitg. 1864, p. 194.

case of numerous Monocotyledons and Dicotyledons, those bundles in any cross-section, which are the first to originate, are also the first to receive the definitive primitive elements of phloem and xylem, does not exclude these possibilities, which are rather to be tested by further investigation.

So far as is known at present, both origination and completion proceed in the acropetal direction in all root-bundles, in all cauline bundles, and in those in the stem of Filices and Marsiliaceæ. The leaf-trace bundles of the Phanerogams certainly do not all show the same behaviour. In Tradescantia albiflora, and in species of Potamogeton—with the exception of the lateral bundles of P. crispus—they are both originated and completed in acropetal order of succession, so far as my investigations extend. In Cordyline and Chamædorea many bundles of the leaf-trace appear, according to Nägeli [1], to take the same course of development. Falkenberg [2] makes the same statement for all Monocotyledons investigated by him.

According to Schmitz [3] the median bundle of the leaf-trace of Berberis vulgaris shows the same acropetal progression, at least as regards its origination; this takes place by means of longitudinal division of a strand of primary meristematic cells, '*starting*' from the point where the median strand of the leaf perpendicularly below (in $\frac{2}{5}$ Phyllotaxis, the sixth) curves outwards. The same holds good, according to Nägeli [4], for the external leaf-trace bundles of Bougainvillea spectabilis, as to which however it is doubtful whether they belong to this series. Frank's statements [5], according to which the same conditions are said to exist in the origination and completion of the trace-bundles in Taxus, Quercus, and Æsculus, require testing.

On the other hand, it has been shown by Vöchting in the case of the bundles of the leaf-trace of the Melastomaceæ, that with regard to both of the processes in question they grow downwards in the basipetal direction from the point of exit in the node. The same conclusion follows from Sanio's investigations in the year 1864 of the bundles of the Piperaceæ, if these, as Weiss [6] maintains, are bundles of the leaf-trace. The definitive completion, at any rate, takes place in very many bundles basipetally from the node of exit; Nägeli states this for a portion of the trace-bundles of Chamædorea and Cordyline, and for those of a very large number of Dicotyledons and Conifers; and it is not difficult here, in growing ends of stems, directly to see the basipetally progressive completion of the tracheæ; comp. e. g. p. 258, Fig. 115, m_4. Thus, as above remarked in demonstrating the course of the bundles in these numerous cases, as we follow them downward from the node, we at the same time follow their order of development.

The possibility that the development of a leaf-trace bundle may follow different directions in different parts of its course, has been discussed by Mohl [7]; in the case of the leaf-trace bundles of the Palm-type, he states that they are developed basipetally from the node in their upper part, but does not consider that this excludes an acropetal development of the lower part. Neither do Nägeli's and Falkenberg's observations, so far as they have been published, appear to me to afford a solution of this question. Development proceeding in two directions is indubitable in the

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[1] Beitr. *l. c.* p. 37.
[2] *l. c.* p. 162.
[3] *l. c.* (see below, p. 393), p. 30.
[4] *l. c.* p. 121.
[5] Botan. Zeitg. 1864, pp. 180, 411.
[6] Cf. p. 250.
[7] Verm. Schriften, p. 181.

case of the lateral leaf-trace bundles in the stem of Potamogeton crispus. It begins here, as already indicated at p. 275 and in Fig. 125, with the appearance of the first tracheides in the node, and advances from the latter, on the one hand, towards the leaf, on the other hand basipetally in the adjoining internodes. Soon after the latter basipetal development has begun, there appear, above the node, in connection with the tracheides in it, the first tracheides of the portion of the lateral strand running through the next internode, and these continue their development in the acropetal direction. The two processes go on in opposite directions in every internode, and meet about half-way up the latter, thus bringing the strand of primitive tracheides into continuity; the acropetal part starts earlier and grows slower than the basipetal. The first origination of the bundles takes place, so far as could be decided, in the acropetal direction.

The completion of the leaf-trace bundles in Equisetum[1] goes on, in a certain sense, conversely to that in the case just described. It begins in the internode while it is still very short, and in fact the primitive elements of the phloem first appear rapidly in basipetal succession, then the first tracheides appear almost simultaneously throughout the entire length of the internode. At a later period the development of the primitive elements proceeds further and in fact upwards into the leaf, and downwards to form the limbs, which are attached to the strands of the next lower internode.

For the more complicated phenomena in the Phanerogams and Lycopods possessing an axial bundle, and leaf-bundles laterally joining on to it, comp. Sects. 70, 77, and 78, 107, 109, 110; Nägeli, *l. c.* pp. 38, 53, 56.

Sect. 116. If a leaf-trace consists of more than one or two bundles, and if, as in the great majority of cases, a median bundle is to be distinguished from lateral ones, it is the rule for the median bundle to be first originated and completed, the lateral bundles being the later developed the more distant they are from the median one. Examples of this have already been given in Sect. 61. The converse order of succession occurs but seldom; as in the leaf-traces of Humulus[2], and of Phaseolus, which have three bundles. Leaf-traces of Monocotyledonous plants with very numerous bundles ranged in several rows in the node, behave, according to Nägeli's investigation of Chamædorea and species of Cordyline, in agreement with the main node; but as regards the succession of the rows they differ in particular cases. Not unfrequently the formation of the lateral bundles of a leaf-trace only starts when the median bundles of several upper leaves are already present. If bundles of the leaf-trace and cauline bundles are both present, the origination and completion of the former takes place as a rule earlier in the same cross section, than that of the cauline bundles. A conspicuous exception to this rule is presented by the Rhipsalideæ with winged stems[3].

In recent times the question has been discussed, with reference to the original differentiation of the meristem spoken of in the Introduction, what is the morpho-

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[1] Hofmeister, Vgl. Unters. p. 93.—Cramer, Pflanzenphys. Unters. Heft. 3, p. 26.—Nägeli, Beitr. I. p. 38.—Russow, Vgl. Unters. p. 145.

[2] Nägeli, *l. c.* p. 114.

[3] Vöchting, *l. c.*

logical region of development of the vascular bundles in the stem[1]. For the axial bundles, as has repeatedly been said above, it is established that their initial strand is the plerome cylinder; the bundles running from them into the leaves are formed out of the surrounding periblem. For the cortical bundles the latter also holds good, at least in the great majority of cases. The same has already been stated at p. 22 for the entire bundle-system of the stem of Equisetum.

It follows first of all from these facts, in accordance with the principle more generally enunciated in the Introduction, that in the stem the formation of vascular bundles is not everywhere connected with one and the same primary layer of meristem. This, however, does not yet answer the question how far other bundles or systems of bundles, occupying a definite position in the stem, may arise from definite zones of differentiation of the primary meristem. This is especially the question in the case of the bundles of the ring and cylinder of the stems typical of Dicotyledons and Monocotyledons. For reasons given at p. 20, the Ferns must be passed over for the present.

In stems of the *Dicotyledonous* type the bundles obviously have their origin in an annular zone corresponding to their definitive arrangement. This zone, when the formation of the vascular bundles begins in it, is distinguished by the rapidly succeeding longitudinal divisions, which give rise to them, and by the small width of the cells, at least at definite points, corresponding to the commencement of the bundles. In the adjoining zones, which become converted into pith and cortex, the longitudinal divisions, from an early period of development onwards, take place more rarely, and cease sooner, if those cases where groups of sclerenchymatous fibres are formed be left out of consideration; the cells, which for the most part become developed into parenchyma, follow the general growth in the transverse direction chiefly by increase of volume without divisions; and this in general takes place in such a manner that the more considerable increase of volume begins in the middle of the pith. The rapid longitudinal divisions of the bundle-ring always begin, on any cross-section, at those points where, in correspondence with the general rules of succession, the first vascular bundles originate: thus, for example, in a young internode, in the position of the single, or of the median trace-bundle going to the next leaf above. Here there first appears in cross-section a small group of narrow cells, proceeding from the division of two, or not many more, original cells, which gradually increases by means of farther divisions corresponding at each time to the thickness of the initial strand, the cross-section of which is represented by this group.

At the side of, or between the first initial bundle-groups of any cross-section the commencements of new initial bundles then appear, in the same form, and in the order corresponding to the general rules for the succession of bundles, and to the course of the leaf-trace in the particular case, until the definitive number holding good for the bundle-ring in question is complete. In particular cases the rapid longitudinal

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[1] Sanio, Botan. Zeitg. 1863, p. 356 &c.; 1864, p. 192 &c.; 1865, p. 165 &c.—Hanstein, Die Scheitelzellgruppe, &c. (1868); cf. p. 7.—Russow, Vergl. Untersuchungen, p. 177 &c.—Vöchting, Melastomeen und Rhipsalideen; compare pp. 259 and 261.—Schmitz, Entwickelung d. Sprossspitze der Phanerogamen, Halle, 1874.—Falkenberg, Monocotyledonen, *l. c.*

division remains confined to the initial bundles of the leaf-trace; broad bands of meristem lying between them take little part in the division, and follow the general growth chiefly by increase in volume of the cells, as in the case of Cucumis, according to Sanio; in the Ranunculi, often mentioned above, the same conditions may exist. In most cases however the cells of the whole bundle-ring, including the bands lying between the leaf-trace bundles (primary medullary rays), remain or become narrower on the average than those of the pith and cortex; the rapid longitudinal divisions extend from the lateral edges of the initial bundles sideways in the direction of the ring, so that bundles of the leaf-trace, which arise later, may be differentiated within a small-celled annular zone already undergoing active longitudinal divisions; e.g. in the Melastomaceæ. In the numerous cases belonging to this category where the bundles of the leaf-trace are early united by numerous intermediate bundles, the rudiments of the former, in consequence of rapid longitudinal division spreading laterally, amalgamate at once at their edges to form together, as it were, a narrow-celled ring, in which the intermediate bundles successively differentiate themselves from the medullary rays which separate them. The origination and completion of the bundles of the leaf-trace here passes over continuously and insensibly into that of the intermediate bundles. Comp. Chap. XIV.

For the origination of the groups of sclerenchymatous fibres the same holds good as for the vascular bundles, in respect of the rapid longitudinal divisions going on in the cells of the primary meristem, and the small width of the elements resulting from this. Where the two occur in company, as so often happens, the breadth of the narrow-celled-ring is essentially influenced by this fact.

To the narrow-celled initial bundle-ring, the not very happily chosen name of Thickening-ring has been applied by Sanio.

With reference to the question put more generally above, we have now further to ascertain what is the morphological region in which (to speak shortly) that initial ring appears. Sanio, on the basis of careful investigations of successive cross-sections, has propounded the doctrine that close below the growing-point the originally homogeneous meristem first becomes differentiated into an axial strand, the '*primary pith*,' which developes into the pith-cylinder of the shoot, and is distinguished by relatively rare longitudinal division and rapid increase in size of its cells, and secondly an external zone surrounding this. The latter again becomes differentiated into a peripheral zone, which forms the outer cortex together with the epidermis, and an inner zone, its thickening-ring. The outer zone, divided into the two layers mentioned, is further that from which all foliar structures are derived. Russow maintains essentially the same view, calling Sanio's primary pith Endomeristem, the zone surrounding it Exomeristem; the latter is divided into the Mesomeristem, which is the inner layer producing the vascular bundles, and the Perimeristem, which is the outer zone, forming the external cortex and the Dermatogen. Endistem, Existem, Mesistem, and Peristem are abbreviated expressions for these successive layers. Thus, according to this view, the entire system of leaf-trace bundles, together with the outer cortex of the stem, as well as the leaves, would proceed in typical Dicotyledons from the existem, or the zone surrounding the primary pith, as is actually the case in Equisetum. Hanstein's discovery of the separation of the primary meristem in the growing-point into the distinct layers called Dermatogen (Epidermis), Plerome,

and Periblem (p. 7), was unknown to Sanio, although he himself first clearly described this phenomenon for some special exceptional cases; Russow opposes this view, and especially the further conclusions drawn by Hanstein, chiefly on the ground of the phenomena in Equisetum.

Hanstein, in his paper of the year 1868, founded the doctrine that the leaf-trace bundles of the typical Dicotyledonous stem are formed in the periphery of the plerome-cylinder, while its central part becomes the pith; and that the periblem (together with the dermatogen) forms all the lateral members, especially the leaves and the outer cortex, as well as the portions of the bundles, which pass through the latter on their way to the leaves and branches. According to this, every leaf-trace bundle is derived in its cauline portion from the plerome-cylinder, in the portion going out into the leaf, from the periblem mantle. Considering the contradiction between this view and that of Sanio and Russow, and in view of the fact already mentioned at p. 8 that the differentiation of plerome and periblem in the growing-points of stems cannot always be traced up to the extreme apex, it might at first be asked whether Hanstein's view of the matter be not incorrect, in so far that the boundary between his plerome and periblem might run, not between the primary meristematic layers above-mentioned, but between those which are only secondarily severed from one another, which Russow calls Peristem and Mesistem. This question or conjecture is however negatived, even wholly apart from stems with an axial bundle ending in a sharply defined plerome-apex, as Hippuris (p. 8), on inspecting longitudinal sections of many growing-points of stems.

In the growing-point of Berberis vulgaris, where the plerome is well distinguished from the single-layered periblem, Schmitz has recently investigated the origination of the leaf-trace bundles, and proved that this takes place in the outer layers of the plerome, but not even at its outer boundary, as the one or two outermost layers take part in the formation of the external cortex. In the apex of the shoots of Menispermum canadense, according to the same observer, it is the external surface of the plerome bundle, here also surrounded by an originally single-layered periblem, in which the vascular bundles originate. In Ephedra, according to Schmitz, a certain decision of the present question is not attainable, on account of the less sharp original severance of the primary layers of meristem.

There are thus indubitable cases among stems of the Dicotyledonous type where the portion of the leaf-trace bundle running through the stem arises from the plerome, and these cases are without doubt numerous. Although, considering the different behaviour of Equisetum, it may be open to objection to base a principle of general application on the existing results, before more numerous special observations have been undertaken, yet provisionally, and in reservation of further researches, a generalisation of the results obtained for cases with a similar type of structure and growth is demanded. For the Dicotyledons in question, therefore, the origin of the leaf-trace bundles, and of the bundle-ring generally, will have to be referred to the outer part of the plerome strand; and, according to Schmitz's observations on Menispermum and Berberis, this will also apply to the fibrous strands and rings which accompany the bundles. As however the bundle-rings of the Dicotyledonous type may no doubt be regarded as everywhere morphologically homologous—at least until the contrary should be proved—and as further the vascular strand, or, which is

the same thing, the plerome strand of the main root is continued directly through the hypocotyledonary axis into the bundle-ring of the stem, we can go a step further, and, in agreement with van Tieghem's view[1], may draw the external boundary of the plerome strand close outside the external boundary of the bundle-ring, even in those cases where the former cannot be distinctly traced into the apex of the primary meristem. According to this view the plerome would be the axial cylinder, which in the first series of cases only becomes marked off from the periblem by the differentiation of the initial cylinder in its external part, and which in the other series of cases is continued with a sharp boundary into the extreme apex of the stem, where it shows no differentiation other than the primary layers of meristem. Among the Angiosperms it appears to be chiefly plants with a very flat apical meristem, forming new internodes at definite intervals, which belong to the first category, while the second includes those with a more elongated apex. With the latter are further connected the elongated apices of plants with one axial vascular bundle, which arises from a sharply defined plerome-bundle.

Medullary bundles situated inside a distinct ring require, after what has been said, no further explanation with reference to their origin from the primary rows of meristem. For the net of bundles in the stem of Gunnera the same holds good, according to Reinke[2], as for the ring of typical Dicotyledons. The Nymphæaceæ and Auriculas require still more accurate investigation with reference to the question under discussion.

For the *Monocotyledons*[3] the question before us may be generally answered by the statement that the cylinder containing the bundles, defined in this sense above at p. 261, is derived from the plerome strand. This is often to be traced into the extreme apical meristem, e. g. Grasses, Polygonatum, Canna, Potamogeton, Tradescantia sp., Asparagus[4]; or it may only be differentiated below this, e. g. Epipactis, &c., according to Falkenberg. The outer layer of the bundle-cylinder, in which the lower ends of the bundles lie, falls in the outer boundary of the plerome, or lies within it. The succession of development of the bundles follows the general rule here also. In consequence of this, and of the course of the bundles described above, we find them, in the case of the Palm-type, appearing in centrifugal order as seen in successive cross-sections of young internodes, the median bundles which penetrate most deeply appearing first, and so on. The completion of the tissue surrounding the bundles, especially the cessation of longitudinal divisions, and the increase in volume of the meristematic cells which become converted into parenchyma, proceed in the same order; in the external region, partly for the reasons already given, relatively more abundant longitudinal divisions and smaller growth of the elements in the transverse directions take place. As long as the longitudinal divisions, which cease in centrifugal order, persist, the periphery of the cylinder is occupied by a meristematic narrow-celled ring, which Sanio identifies with his thickening-ring demonstrated in the case of the Dicotyledons, a view which is so far, but only so far correct, as both constitute that zone of the plerome body which is engaged in differentiation and in the formation of vascular bundles.

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[1] Ann. Sci. Nat. 5 sér. tom. XVI. p. 112, note. [2] Morpholog. Abhandl. p. 67.

[3] [Compare Guillaud, Ann. Sci. Nat. 6 sér. Bot. tom. V. pp. 1–176.]

[4] Hanstein, *l. c.*—Falkenberg, *l. c.*

A necessary consequence of the view here propounded is that in the Monocotyledons also every leaf-trace bundle arises from the plerome as regards that portion which passes through the cylinder, but from the periblem as regards that portion which runs out into the leaf.

As regards the origination and completion of the individual bundles in the leaves themselves, essentially the same rules hold good as in the case of stems. That their initial strands of meristem must have a definite position and orientation, and that the latter must correspond to that of the mature bundle, is obvious[1]. The longitudinal progression of their origination and completion is guided by the direction of growth of the leaf, which, as is well known, varies in the particular cases.

That the bundles of lateral buds connected with the system of the main axis originate later than the latter, scarcely requires to be mentioned; their development, or at least their completion, either proceeds centrifugally, i.e. from the point of attachment onwards into the lateral shoot, e. g. Potamogeton, Fig. 123, p. 273; or in the opposite centripetal direction, e. g. in the node of Zea and Saccharum.

Sect. 117. The development of normal lateral roots on a relative main root is so immediately connected with the development of the vascular bundles of roots, at least in the case of the Phanerogams, that it cannot be wholly passed over in this place, although, strictly speaking, it belongs only in a small degree to the subject of this book.

In the *Phanerogams*, as shown by Nägeli and Leitgeb, Reinke and Janczewski[2], from the last of whom the following summary is principally taken, the young pericambial layer is the chief seat of formation of normal branch-roots; neighbouring layers of cells may take part in the process to a varying extent. How far the latter takes place is determined according to the particular cases to be adduced, and these correspond in a great degree, though not always with accuracy, to the types of differentiation of the apical meristem enumerated at p. 9, &c.

We have here to assume as already known, that the rudiment of monopodial branch-roots always arises upon the axial bundle of the relative main root, that it here acquires its characteristic structure, especially the differentiation of its growing-point, and then, boring through the peripheral layers of tissue, reaches the surface.

Among the Phanerogams investigated, Janczewski distinguishes five types of the processes of development in question.

In the *first* of these, to which only Pistia belongs, the plerome-cylinder and the periblem of the lateral root are derived from the growth and corresponding divisions of the single-layered pericambium; the root-cap, or calyptrogenic layer, and the epidermis, are derived from the endodermal layer. In the *second* type, represented by Alisma Plantago, Sagittaria, and Zea, the entire lateral root, including the calyptrogenic layer, arises from the pericambium, the divisions of which begin irregularly. The endodermal layer only forms an exterior coating on the cap, and, in the case of Zea, also the epidermis and outermost cortical layers at the base of the lateral roots. With reference to the participation of the layers of the mother root,

[1] Compare p. 23.

[2] Nägeli and Leitgeb, Entstehung u. Wachsthum d. Wurzeln, Beitr. zur Wissensch. Botanik, Heft 4.—Reinke, in Hanstein's Bot. Abhandl. Heft 3; id. Morpholog. Abhandl. p. 1.—Janczewski, Ann. Sci. Nat. 5 sér. tom. 20.

Janczewski's *third* type (Fagopyrum, Raphanus, Helianthus) stands near the second, inasmuch as the entire rudiment of the lateral root arises from the pericambium, with little or no participation of the endodermal layer. It is distinguished from the second type by the regularity of the initial divisions. The cells of the segment of the pericambial layer concerned, become elongated in a radial direction, and divide once tangentially. The inner of the two layers derived from the latter division forms the commencement of the new plerome bundle; the outer is divided again tangentially into an outermost layer, which is the calyptrogen, and an inner, or middle layer, which forms the commencement of the entire cortex. In Helianthus the endodermal layer of the mother root forms a many-layered external covering to the root-cap, over the apex of the rudiment of the lateral root; in Fagopyrum it only grows to form a single-layered envelope of the latter; and in Raphanus it remains quite passive.

In the *fourth* type, which embraces the Cucurbitaceæ and Papilionaceæ mentioned at p. 12, the rudiment of the lateral root is derived from the common growth of the portion of the pericambium in question, of the endodermal layer, and of the 1–2 cortical layers adjoining the latter externally. The former constitutes the plerome bundle, the latter conjointly form the surrounding portions of the rudimentary root, under the apex of which the common initial zone is differentiated at a relatively late period.

The roots of Pinus constitute the *fifth* type. The whole rudiment of the lateral root, which soon assumes the differentiation described at p. 13, proceeds from the many-layered pericambium; the endodermis and the layers adjoining it externally remain passive. In the Cycadeæ, in Taxus, and in Sequoia, on the other hand, the latter, according to Reinke and Strasburger, take part to a small extent in the formation of the most peripheral layers of the rudimentary root[1].

In opposition to the Phanerogams the lateral rudimentary roots, in the case of the monopodially branched roots of all investigated *Ferns* and *Marsiliaceæ*[2], take their origin from the endodermal layer which surrounds the pericambium; in the *Equiseta* they arise from the layer lying within the endodermis (comp. p. 351). In many Cyatheaceæ and in Marsilia the longitudinal rows of endodermal cells, which may be shortly described as rhizogenetic rows, and which, as corresponding to the places of origin of the lateral roots, face the xylem-plates, are distinguished by their wider and shorter cells from the other rows of the same layer; frequently those rows of the next outer cortical layer, which lie in front of the rhizogenetic rows, show similar relations of size, and also have their walls less thickened than the other rows belonging to the same layer. The layers however which lie outside the endodermal layer take no active part in the origination of lateral roots. On the contrary, every lateral root proceeds from a cell belonging to the rhizogenetic layer, which directly, or after a few irregular preliminary divisions, assumes the characteristics of the apical cell of the root, as described at p. 18. The pericambium of the mother-root is only concerned in the formation of lateral roots, in so far as the connecting piece between the vascular bundles of the two orders is formed in it.

As already indicated, the place of origin of a lateral root in the Ferns and Equisetum is always a circumscribed portion of tissue lying in front of a xylem-plate.

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[1] Strasburger, Die Coniferen, &c., p. 348.

[2] Nägeli und Leitgeb, *l. c.* p. 88.

In those Phanerogams, in which the pericambium extends over the external corner of the xylem-plates, the same holds good, with the exception of Lycopersicum. In these cases therefore a longitudinal row of the rudimentary roots faces each xylem-plate, an arrangement which is always conspicuous even externally in the case of oligarch roots; the attachment of the vascular bundles takes place in the form described above at p. 387. Where, on the other hand, the xylem-plates of the roots of Phanerogams directly abut on the endodermis, as is the rule among the Grasses, the rows of rudimentary lateral roots alternate with the xylem-plates, and lie opposite the centre of the phloem-bands, as was stated at p. 387.

According to van Tieghem's investigations the rhizogenetic longitudinal bands, and the products of their development, have the same position in the case of the Pittosporeæ, because a group of oil passages here lies in the pericambium in front of each angle of the xylem, as is to be stated in Chap. XIII. As also described in that chapter, in the case of the Umbelliferæ and Araliaceæ, e.g. Hedera, an annular row of oil or resin passages likewise lies in the same position, but here a quite similar passage is also present in front of each phloem-group. It is therefore the rule for these plants, apart from individual exceptions described by van Tieghem, *l. c.* p. 149, that on each side of every angle of the xylem, alternating with the latter and the next phloem-group, there lies a rhizogenetic pericambial band; thus the number of these bands, and the rows of lateral roots is double that of the xylem-plates, and the attachment of the bundles of the latter takes place as described at p. 387[1]. In Lycopersicum, as already stated, the same condition occurs, without any assignable anatomical ground.

At the conclusion of this chapter it will be convenient to justify some of the opinions here expressed, in opposition to other views.

In the first place, *with a view to simple matters of fact*, every distinct strand, which is separate from others of identical or similar structure, and which consists of tracheæ or sieve-tubes, has been designated by the name vascular bundle; to the typical complete strands of this kind, those which remain or become incomplete were appended. This usage is based on the nature of the object, for the fact is established that the two essential forms of tissue, tracheæ and sieve-tubes, together form these bundles. If the principle maintained in this book, of distinguishing and regarding the systems of tissue, with reference to the forms of tissue which compose them, were carried out with extreme consistency, the phloem of the bundles would no doubt have to be considered separately from their xylem, while the further elements belonging to the bundle would again demand a distinct treatment. It will scarcely however be disputed, that this would not only confuse the description, but also misrepresent the relations which actually exist. If the bundle formed of tracheæ and sieve-tubes as its essential constituents, or even each of its two parts, containing one of the essential forms of tissue, be regarded as a whole, it is obvious that the non-equivalent organs, such as parenchymatous cells, &c., which occur in it, must also be reckoned among its elements. If the comprehension of non-equivalent elements is thus once conceded, it may further be extended to those which lie *outside*, that is, at the periphery of the essential tissues. As soon as this has been done, strict limitation according to the principles above laid down is, it is true, given up; the actual boundary of the vascular bundle becomes conventional, though this conventional limitation may be based upon good grounds derived from other considerations, as from that of the primary differentiation of the meristem. It will be so far admissible as, on the one hand, the weight of these reasons, and on the other, advantages

[1] See van Tieghem, *l. c.*; and Canaux sécréteurs, Ann. Sci. Nat. 5 sér. tom. XVI.

in comparative anatomical description, can be brought to bear in its favour. The limitation of many vascular bundles by means of the endodermis, to which we have adhered in preceding paragraphs, that is to say, the view that the boundary of the bundle is to be drawn at the inner surface of the latter, is, for example, conventional in the sense indicated. In the bundles of roots this limitation has a genetic basis, in so far as the endodermis is the innermost layer of the periblem, while that which it encloses proceeds from the plerome. In other cases, as in the leaves of the Primulas, this developmental ground is absent; in the case of many bundles of Ferns, developmental considerations in themselves undoubtedly lead to the opposite result, as the endodermis and the adjoining layer of the bundle are here derived, relatively late, from the division of one layer of mother-cells. Nevertheless, on more extended comparison, the limitation of the bundle on this principle will hardly be disputed. It is further purely conventional, but, as in the example previously adduced, justified by developmental considerations and in the interests of clearness, when the pericambium and the parenchymatous layers within the endodermis of concentric bundles in Ferns are included in the bundle and not treated as separate sheaths.

The same, or at least quite similar, considerations may be applied to the fibrous strands, the 'bundles of bast-fibres,' which accompany many vascular bundles. There is simply no decisive reason to be found for placing the boundary of a bundle, which they accompany, at their external, or at their internal surface. Where they accompany the vascular bundle, they form with the latter one whole, and the fact that they are completed later than the first, or than many of the elements of the vascular bundle, is in itself no ground for separating them from the bundle, for the essential elements of the latter also attain completion in a definite succession. It is here also conventional, if, as was done above, the fibrous strands are separated from the vascular bundles, and if the boundaries of the latter are drawn on the inner side of the former. The ground for this conventional limitation, however, lies in the fact that the accompanying fibrous strands consist of a sort of tissue different from the essential tissues of all vascular bundles, that they are absent from very many vascular bundles, and are thus non-essential for the vascular bundle generally; and lastly that they, in a still higher degree than the endodermal sheaths, belong to a form of tissue, which in itself forms a system quite independent of the vascular bundles, and which, in its development, does not stand in any constant relation to the primary differentiation of the meristem. They are portions of a system which may, but which need not, directly accompany the vascular bundles, and they must be included in this system; it is therefore well to separate them once for all from the vascular bundles. These considerations may also throw light on the discussion which has often been carried on in recent times, and which very clearly illustrates the confusion of ideas now prevailing in the field of anatomy, as to whether the accompanying fibrous strands belong to the 'fascicular tissue' or to the 'ground tissue[1].'

The limits between the vascular bundles themselves can be fixed with less difficulty than those between the vascular bundle and its surrounding tissue. If we have once distinguished as a vascular bundle that distinct strand which is formed of tracheæ and sieve-tubes definitely grouped, this distinction must be carried out universally, both for the sake of consistency and in the interests of clearness, and *every* distinct group of the two kinds of organs in question, which forms a united whole, must be called a vascular bundle. What the special grouping of the essential organs may be in these cases, whether the bundle has arisen from the union of several, whether in any one case it corresponds as regards position and origin to a system of numerous bundles which occurs in other cases, these are in themselves questions which have their importance, but they do not touch the anatomical distinction under consideration. On these grounds, the axial bundle of roots, and of the stems of Lycopodiaceæ, has been treated as *one* vascular bundle. It is here also conceded that the subject may be regarded from other points of view, and thus, for example, we may cease calling the axial bundle of roots a vascular bundle, and regard it

[1] [Compare Guillaud, *l. c.* (see p. 396).]

rather as a central cylinder or plerome-strand differentiated into tracheal plates, phloem strands, pericambium, &c. But this method, if consistently carried out, must lead at once to that general breaking-up of the vascular bundle, which, as already stated above, though completely justified in principle, is certainly not desirable in the interests of clear description.

With reference, secondly, to the *Terminology* employed, I have, as will be granted, aimed at the greatest possible simplicity and clearness of expression, and endeavoured, as far as possible, to preserve or to restore names of long standing. I must apologize for the single really new word, Epithema; it is not pretty, but I could not find a better one. The reasons for keeping or not keeping most of the names which come into question follow partly from what has just been said, partly from the necessity of being consistent in exposition, while they have in part been expressly stated in the latter. It would lead us too far, and would not be interesting, to discuss them all severally in this place. My motive for substituting the old expression vascular bundle for the term fibro-vascular bundle, which has lately become more usual, has likewise been generally stated above, partly at pp. 232 and 318, partly in the earlier portion of this note. In fact vascular bundle, in the above description, denotes something different from Nägeli's expression Fibro-vascular strand, inasmuch as the latter comprehends the accompanying fibrous tissue, which has been excluded from the vascular bundle above. A vascular bundle may appear as an essential part of a fibro-vascular strand, but it is not necessarily, and very often not actually combined with accompanying fibrous tissue, and the two things must therefore be distinguished. I have preferred the expression vascular bundle to the more recent 'conducting bundle,' because it is the traditional term, which is also preserved in the phrase fibro-vascular strand, and because no decisive ground appears to me to exist for laying aside the old convenient word, which correctly indicates the principal point, or for limiting its application.

Caspary [1] has adopted the latter course, and has distinguished the bundles containing tracheides, under the name of 'cellular conducting-bundles,' from those which contain vessels, and comprehended both under the name conducting-bundle, because he assumed a great difference between tracheides and vessels, like that between cells and vessels. As the distinction between the two forms of organs is actually a very trifling one, the ground for the sharp severance of the two kinds of bundle, and thus for the change of name, in my opinion disappears. It is no doubt an inaccuracy which is permissible in the interests of simplicity of expression, to speak of vascular bundles without vessels, i. e. bundles in which the latter are replaced by tracheides.

[1] Berliner Acad. Monatsber. 10 July, 1862, p. 453.

CHAPTER IX.

ARRANGEMENT OF THE PRIMARY PARENCHYMA.

Sect. 118. The primary parenchyma, in so far as it is not a constituent of the vascular bundles, forms, as often indicated in earlier chapters, the principal contents of the space enclosed by the epidermis, where it is left free by the vascular bundles. Within this space it is traversed by other, non-equivalent forms of tissue, as will be stated in succeeding chapters. The regions characterised in the preceding pages as external cortex, pith, and medullary rays, as well as the leaves and foliar expansions, are therefore, as regards their main mass, built up of parenchyma.

Within the limits of this general plan, however, definite rules exist for the distribution and arrangement of the particular forms of parenchyma distinguished in Chap. I, Sect. 3, and these rules will be here given. In doing so, attention will chiefly be directed to the relatively thin-walled forms, and we shall return to the sclerotic forms in the next chapter, on account of their close anatomical and physiological relations to the sclerenchyma. As the occurrence and distribution of the different individual forms is chiefly determined according to the various organs of the highest degree in which they occur, and to their anatomical regions as distinguished in the previous chapter, it is expedient to classify the description with reference to these organs and regions, in such a manner that first the parenchymatous masses characteristic of each will be described, and then their limiting and sheathing layers.

Sect. 119. The parenchyma of the *pith* and of the *bundle-cylinder* of the stem consists in general of cells arranged chiefly in longitudinal rows, without any very remarkable anatomical peculiarities; when young they contain products of assimilation, and in foliage shoots frequently chlorophyll, and they either preserve this condition of their contents throughout life, or, as is especially the case in Dicotyledons, they soon dry up and die off. In the pith of many Dicotyledons, the two conditions occur in different rows of cells, which then also differ with respect to the form and size of their elements, as is shown by the examples of ligneous plants investigated by A. Gris, which are to be cited below. From the earliest period of development onwards, intercellular spaces containing air appear in the pith, which sometimes persist in the form of narrow interstices, sometimes form wide lacunæ, while in the numerous cases of stems which become hollow in the internodes, owing to their cells dying off, they are widened to form the axial air-canals described above. Cf. Sects. 51, 52.

In most stems belonging to the Dicotyledonous type, the elements of the pith, as stated in Sect. 116, become narrower towards the inner boundary of the ring of bundles; together with the innermost portions of the vascular bundles, they here con-

stitute the zone distinguished as the medullary sheath, to which we shall have to return in Chap. XIV. In like manner the parenchyma of the cylinder of bundles in Monocotyledons becomes as a rule narrower-celled towards the outer surface of the latter. In those stems of Dicotyledons and Equiseta which become hollow, the narrower peripheral elements of the pith are persistent; the case is the same in the Monocotyledons for the elements of the entire zone which surrounds the cavity and contains the bundles.

According to the comparative investigations of A. Gris[1], the pith of Dicotyledonous ligneous plants at first consists entirely of parenchyma, in which crystal-sacs appear constantly, and sclerenchymatous elements not unfrequently. On the complete development of the one-year-old stem or branch, the cells of the parenchyma sometimes become emptied of their contents, and then dry up, so as to contain air (empty cells, 'cellules inertes' of Gris); sometimes they remain as active parenchymatous cells (cellules actives), which alternately store up and give back products of assimilation, especially starch and tannin, according to the periods of vegetation. According to Gris, this activity continues for years; in the case of Platanus occidentalis, Gleditschia ferox, Betula alba, Quercus Robur, and Fraxinus, it has been traced as far as the 20th year of life. The active cells are, as a rule, distinguished from the empty ones by their smaller size, and their thicker, finely-pitted walls.

Only in a few woods does the pith become entirely empty and dried up: Sambucus nigra. In most cases it either consists of active cells, with crystal-sacs which are isolated or distributed in larger groups, or of these elements and empty cells in varying arrangement. The former is termed by Gris homogeneous pith. This occurs with a relatively small number of isolated crystal-sacs in very numerous ligneous plants; as in the investigated species of Pyrus, Cydonia, Aronia, Quercus, Fagus, Betula, Alnus, Platanus, Ilex, Prinos, Buxus, and many Ericaceæ; it is interrupted by larger scattered groups of thin-walled crystal-sacs, which are isolated, or arranged in a reticulate manner as seen in cross-section, in Pernettya, species of Rhododendron, Calluna vulgaris, Andromeda polifolia, Cladothamnus, &c.

Pith, which is compounded of active and empty cells, is called by Gris heterogeneous. It is composed either of an empty central and an active peripheral portion, as in Lonicera fragrantissima, Abelia rupestris, Symphoricarpus vulgaris, Ligustrum, Ornus, Syringa vulgaris, Berberis vulgaris, Ulmus campestris, Celtis, and Rhamnus sp.; or this arrangement is complicated by the occurrence of active bands in the central empty portion: Pyrus Malus, Sorbus Aucuparia, Aria torminalis, Cratægus Oxyacantha, Amorpha glabra; or it is everywhere made up of alternating bands of empty and active tissue, in which case the latter chiefly forms longitudinal rows: Viburnum Tinus, and Lantana; or bands anastomosing in all directions in a reticulate manner: Rubus, Rosa[2], and Clethra; or diaphragm-like transverse plates: Magnolia, and Liriodendron. In the nodes and at the boundary of successive annual shoots, the pith is on the whole tougher, and in the heterogeneous forms has a larger proportion of active elements.

With regard to further details, for which reference is to be made to Gris, a great constancy of structure exists for each species. The examples mentioned of Rosifloræ and Ericaceæ show that species of like habit, belonging to closely-allied genera of a family, may behave differently.

In the parenchyma of the primary *medullary rays* essentially the same conditions

[1] Sur la moelle des plantes ligneuses, Ann. Sci. Nat. 5 sér. tom. XIV. p. 26, pl. 4–7.—Nouvelles Archives du Muséum d'Hist. Nat. VI. p. 201.

[2] Compare Mohl, Poren d. Pflanzen-Zellgewebes, p. 27, figs. 27, 37, 38.

prevail as in that of the periphery of the pith. The peculiarities which come under consideration in the case of stems with secondary formation of wood, are to be compared in Chap. XIV.

In most cases, and especially in those cases forming the rule, in which the stem bears well-developed foliage-leaves, the *outer cortex* of the stem is built up of two more or less distinct parts; one, the *Hypoderma*[1], bordering directly on the epidermis, and consisting of thicker-walled, closely united elements, which are often collenchymatous or sclerotic, and in the latter case are still to be described in the following chapter; the other, a thinner-walled, *internal* mass of parenchyma, the cells of which as a rule become successively wider towards the interior, and always leave between them interstices or lacunæ filled with air. Both parts show a different arrangement according to the particular cases. For the Dicotyledonous stem, Schleiden's[2] classification may be adopted, and the following principal forms may be distinguished.

(*a*) The hypodermal layer surrounds the whole stem as a distinct, closed, multiseriate (collenchymatous) layer, which is only interrupted where stomata are present by small gaps leading to the latter: many Cacteæ, Melianthus major, Euphorbia splendens, Syringa vulgaris, Begonia macularis, Ailantus glandulosa, Rosa, Aristolochia Sipho, Piper rugosum, Cacalia ficoides, and Cotyledon coccinea.

(*b*) The collenchymatous or sclerotic hypoderma forms longitudinal bundles, which alternate with longitudinal bands of thin-walled parenchyma, destitute of collenchyma, reaching to the epidermis. The former usually occur in more or less projecting corners of the stem, while the parenchymatous bands lie between them, as in many angular stems, Umbelliferæ, Chenopodiaceæ, Malvaceæ, Solanaceæ, and Sambucus; in other angular stems, e.g. Labiatæ, the collenchymatous hypoderma is massively developed in the angles, between them it is at least weaker in every respect.

(*c*) The epidermis is bordered by a collenchymatous hypoderma, which towards the inside gradually passes over into the thinner-walled, loose mass of parenchyma, and is broken up into isolated masses by the thin-walled parenchyma which extends to the epidermis at the points where stomata occur. So in the primary cortex of most Dicotyledonous woody plants, e.g. Pyrus, Æsculus, Salix, Cupuliferæ, Betula, Acer, Hedera, Tilia, etc., with more or less sharp limitation, and a varying number of strata in the hypodermal layer.

As follows directly from what has been said, the limitation and bulk of the firmer hypodermal layer is very various, even in the preceding typical cases. In weak stems, as in those of many water-plants, it often entirely disappears, and is only indicated by the smaller width and closer connection of the cells bordering directly on the epidermis, as compared with those which lie deeper.

The converse case is more rare, namely that in which thin-walled, loose parenchymatous layers border immediately on the epidermis, while an inner zone forms a many-layered sheath—then always more or less sclerotic—which surrounds the ring of bundles; e.g. species of Papaver and Thalictrum.

On the occurrence of stomata, and their relations to the structural phenomena in

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[1] Compare p. 225. The word Hypoderma was introduced by Kraus; Cycadeenfiedern, Pringsheim's Jahrb. IV.

[2] Grundzüge, 3 Aufl. II. p. 152.

question, Sect. 7, p. 45, is to be compared; on the structure of the collenchyma, comp. Sect. 26, p. 119. The thin-walled parenchyma of the external cortex contains chlorophyll, except in the few plants which are altogether destitute of it, and the nearer the surface, the greater on the average is its amount. As already stated, the parenchyma is always traversed by spaces containing air, and often by wide lacunæ. Also the large lacunæ, chambers, and air-passages in the stems of water-plants (comp. p. 211) lie in the internal parenchymatous mass, and in fact are so distributed that they form a circle, interrupted by radial, usually one-layered lamellæ, between a denser zone immediately surrounding the ring of bundles or axial strand, and the hypodermal zone; or they may be situated in the same region in two or more alternating circles. The former is the case in Myriophyllum, Ceratophyllum, Elatine Alsinastrum, Callitriche, and Utricularia vulgaris; the latter in Hottonia, Trapa, Hippuris, etc.

Generally similar phenomena, which cannot be more fully described here, and to some of which we shall have to return in the next chapter, are shown by the cortex of Monocotyledonous stems. Comp. Fig. 120, p. 269; Fig. 125, p. 274; Fig. 171, p. 369.

In order to avoid repetitions we will return in the following chapter to the cortex of the Fern-like plants, in so far as it belongs to our present subject.

The stems of those chlorophyll-containing plants in which the foliage-leaves are feebly or not at all developed and in which the stems themselves undertake the function of the green foliage[1], and likewise the numerous Monocotyledons with 'halms' similarly constructed to the foliage-leaves of the same plant, behave differently from the ordinary leafy-stems, inasmuch as their cortical parenchyma assumes the structure of those layers of concentically constructed laminæ which contain chlorophyll; this structure will be described in Sect. 121. Examples of this will be given at the place indicated. Comp. also p. 265.

Sect. 120. *Petioles* and stout *ribs of the leaf* show in general a similar structure of the parenchyma surrounding the vascular bundles to that in the stem of the same plants; the layers and bands of thin-walled or collenchymatous parenchyma, and in many cases of sclerotic elements also, are often continued into them from the stem[2]. In the smaller petioles and ribs the collenchymatous or sclerotic elements occur for the most part, or exclusively, around the vascular bundles. Aqueous- and chlorophyll-parenchyma take part in the composition of the larger ones in very various forms. The large petioles of Ferns are especially to be mentioned as examples of the band-like or isolated distribution of air-containing parenchyma, covered by an epidermis containing stomata, and lying between masses—here usually sclerotic—covered by an epidermis destitute of stomata. Most frequently the air-containing parenchyma first-mentioned extends down each side of the petiole from the base of the lamina, in the form of a longitudinal band; in species with a creeping stem, e.g. species of Hypolepis and Pteris, the bands are often continued along its lateral surface throughout its length. In the petioles of Tree-Ferns the bands are frequently interrupted, forming a longitudinal row of short strips; e.g. Cyathea medullaris. On the persistent base of the

[1] [Compare Pick, Beitr. z. Kenntn. d. assimilirenden Gewebes armlaubiger Pflanzen. Diss. Bonn, *Ref.* Bot. Centralbl. 1881, Bd. 6, p. 234.]

[2] Compare Kraus, Cycadeenfiedern, in Pringsheim's Jahrb. IV.

leaf, the pulvinus of the Cyatheaceæ, the air-containing parenchyma appears on the sides and on the dorsal surface in the form of round or oblong, sharply circumscribed, isolated groups, with a breadth and depth of a few millimetres, which consist of a mass of cells shaped like many-rayed stars, leaving between them wide lacunæ, and covered by a portion of epidermis containing stomata. At first narrow interstices containing air lead from the lacunæ into the deeply-seated tissue. At a very early stage of development, in the cases investigated before the petiole and lamina begin to unroll and to unfold, the epidermis and the mass of stellate cells covered by it die off, while the walls of the latter become thickened, and assume a yellowish brown colour; the dead and crumbling mass leaves a furrow behind, filled by its powdery remnants, and this becomes sharply limited owing to the sclerosis of the surrounding multiseriate cellular layer. The latter becomes attached, all round the petiole, to the tough, sclerotic, brown, peripheral cortical layer, and appears in the mature condition as an indented portion of the latter. Comp. Figs. 140 and 141 (p. 292), or Fig. 189 at *f*[1].

We need not enter here into further details of structure of petioles and ribs, but may refer to the next chapter for some special points still to be brought forward.

Sect. 121. The space in the *lamina of the leaf* which is left free by the ribs and vascular bundles, is mainly occupied by parenchyma, which is simply called leaf-parenchyma or in the special case of flat foliage-leaves *Diachyma* or *Diploë* according to Link [2], *Mesophyll* according to De Candolle [3]. In the little-developed scales and cataphyllary leaves, especially those which are destitute of chlorophyll, it shows no general anatomical peculiarities worthy of remark. In the case of the green foliage-leaves special phenomena of structure and arrangement are known, especially since the works of Treviranus [4] and Brongniart [5]. Organs of a different morphological value, which in certain plants assume the functions of foliage-leaves — Phyllodes, Phylloclades, Halms, &c. — behave essentially like leaves as regards the structure of their parenchyma, as has already been to some extent noticed above; for this reason they are likewise to be discussed here.

The parenchyma of the organs in question is, in great part at least, *chlorophyll-parenchyma* [6], in the sense of the word indicated at p. 116; its character and distribution primarily determine the conditions which are to be considered here. With reference to these, two main types are to be distinguished, though they are united by intermediate forms.

1. In the first type, which may be called the *centric*, the chlorophyll-parenchyma is uniformly distributed around the entire organ—if intercalated bands of non-equivalent tissue be left out of consideration. In flat horizontal parts slight differences occur in relation to the upper and lower side.

To this type belong the leaf-like branches and 'Halms,' flat foliage-leaves which are not horizontally placed, and many which are both flat and horizontal.

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[1] Mettenius im Bericht d. 34, Versamml. deutscher Naturforscher, zu Carlsruhe, p. 99.—Von Mohl, Baumfarne (*l. c.*, see p. 291).—Karsten, Veget. Org. d. Palmen, *l. c.*

[2] Philos. Botan. ed. 1, pp. 176, 188.

[3] Organographie, I. p. 271.

[4] Verm. Schriften, I. p. 184; Physiol. I. p. 443.

[5] Recherches sur la structure et la fonction des feuilles, Ann. Sci. Nat. 1 sér. tom. XXI (1830), p. 420, pl. 6–18.

[6] [Compare Haberlandt, Vergl. Anat. d. ass. Gewebesystems, Pringsh. Jahrb. vol. XIII. p. 74.]

The cells of the chlorophyll-parenchyma are arranged below the epidermis in radial and tangential rows; between them there are always spaces filled with air, usually forming narrow interstices. According to the particular cases, to be exemplified below, their form is rounded-polyhedral, or elongated transversely, i. e. parallel to the surface; or elongated-prismatic, or cylindrical, and extended vertically to the surface of the entire organ. According to their shape and arrangement the cells of the latter form have been not inappropriately designated *palisade-cells*, or palisade-parenchyma[1] (comp. p. 117). These cells are of approximately equal height in each of the layers parallel to the surface; between their lateral angles are interstices containing air, which either run without interruption along the whole angle, or form those rows of narrow slits described at p. 211.

The seriate arrangement of the chlorophyll-parenchyma usually becomes less regular at an increased distance from the surface; the palisade-form often passes over into the roundish form.

According to the form in which chlorophyll-parenchyma, and in certain cases non-equivalent masses of tissue, take part in the composition of the entire organ, two principal modifications of the centric type are distinguished, between which here also intermediate forms are found.

(*a*) In many leaves the whole parenchymatous mass is chlorophyll-parenchyma; towards the middle of the leaf this gradually becomes larger-celled, poorer in chlorophyll, looser, and is often even traversed by large lacunæ containing air. To this category belong the leaves, consisting of a few layers of parenchyma, of species of Potamogeton, Ranunculus aquatilis; the leaves of Chamærops, Copernicia, Klopstockia, Physosiphon, Vanda, Cypripedium spec.; many Grasses, as Secale, Elymus arenarius, Triticum vulgare; Yucca filamentosa, with a strongly lacunar central portion; species of Crassula (Fig. 180, p. 378), and Dianthus Caryophyllus. The leaves of the species of Isoetes[2] are also to be mentioned here, with their four air-passages distributed symmetrically over the cross-section, in I. Hystrix and Durieui extending to the epidermis (comp. sect. 51). The leaf of Acorus Calamus, with round-celled chlorophyll-parenchyma in the periphery, and a widely lacunar central portion, may here be mentioned as a transitional form to the second modification. The flat leaves of the first modification described behave in many respects intermediately between the second modification and the bifacial type.

(*b*) The entire organ is built up of a many-layered peripheral zone of chlorophyll-parenchyma, and a dissimilar *middle portion* or *middle layer*, more or less sharply marked off from the former. In the leaf-like stems and halms, all of which, according to what has been said above, belong to this category, this middle portion consists of the ring or cylinder of bundles, to which may be added a surrounding inner zone of large-celled cortical parenchyma, containing little or no chlorophyll (e. g. Salicornia); the chlorophyll-parenchyma forms the peripheral cortical zone; e. g. the halms of Cyperaceæ and Juncaceæ, Acorus, Casuarina, Bossiæa, Mühlenbeckia platyclados, Colletia horrida, Cacteæ, &c.; the Equiseta are also to be mentioned here. In numerous foliage-leaves and phyllodes, especially those which

[1] Schacht, Lehrb. II. p. 118.

[2] A. Braun, Monatsber. d. Berliner Acad. 1863, p. 154.

are succulent and leathery, a middle layer is present, similar to the entire organ in form, which fills up the internal space, and is enclosed by the chlorophyll-parenchyma as by a cortex; in many species of Aloë (A. tesselata, cuspidata, atrovirens, &c.) it breaks through the latter, as it were, in places, so as to reach the epidermis[1]. It consists, as a rule, of relatively large, colourless cells, destitute of chlorophyll, which essentially contain water or sap; in succulent plants, e. g. many species of Aloë (A. soccotrina, plicatilis, arborescens), in other Monocotyledons and in Mesembryanthemum, they contain abundant thin mucilage (comp. p. 116); in sappy leaves they have soft walls, in tough leathery leaves thicker pitted walls. On the course of the vascular bundles within, or at the boundary of the middle layer, comp. sect. 92, p. 305, and sect. 112, p. 378.

Examples of this structure[2], besides those already mentioned, are afforded by

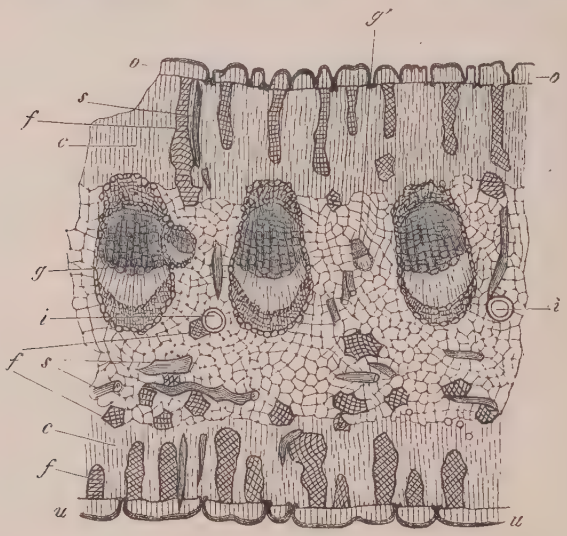

FIG. 187.—Cross-section through the leaf of Welwitschia mirabilis (40). *o* epidermis of the upper, *u* of the lower surface; in their depressions are stomata. *g* trunks of vascular bundles, *g'* small branch bundle; on the trunk marked *g* a similar one is shown branching off. *s* thick sclerenchymatous fibres containing crystals, Hooker's spicular cells; *f* hypodermal and internal strands of long sclerenchymatous fibres; *c—c* delicate palisade-parenchyma, containing chlorophyll. Between *c* and *c* is the wide-meshed tissue of the middle layer. Compare Fig. 55, p. 132, Fig. 145, p. 303, and Fig. 157, p. 335.

the foliage-leaves of many Coniferæ, e. g. species of Podocarpus, Araucaria with flat leaves, Pinus (Fig. 185, p. 381), the leaf of Welwitschia (Fig. 187), the leaves of Myrtaceæ (Callistemon, Eucalyptus Gunnii, Melaleuca tetragona, linearifolia), Proteaceæ (Hakea spec.), Statice monopetala, purpurea; the phyllodes of Oxalis fruticosa and many Acaciæ, &c.; lastly, numerous leaves of Monocotyledons.

Among the special phenomena, which are extremely various in different species, we have first to mention, with reference to the middle layer, that in many flat leaves of Monocotyledons this is divided into as many longitudinal bands as there are longitudinal bundles running through the leaf (p. 301), each of these bundles

[1] Pfitzer, in Pringsheim's Jahrb. VIII. p. 64, fig. 20.

[2] [Compare Briosi, Contribuzione alla Anat. d. foglie. *Ref.* Bot. Centralbl. Bd. 11, 1882, p. 55.]

being inserted in a lamella of round-celled parenchyma containing chlorophyll; these lamellæ unite the chlorophyll-layers of the two surfaces of the leaf, and stand at right angles to the latter; e. g. Hemerocallis fulva, Narcissus pseudonarcissus, Hyacinthus orientalis, Ornithogalum umbellatum, Phormium tenax, many Irideæ, Bambuseæ[1], &c. Secondly, in the leaves of many Monocotyledons, narrow-leaved Eryngia, Lobelia Dortmanna. &c., the middle layer is soon destroyed to form lysigenetic air-passages. In the round-leaved species of Allium and Asphodelus, in which the middle of the leaf is destitute of vascular bundles, a wide tubular cavity traversing the leaf arises in this way; in leaves where the vascular bundles are inserted in persistent plates of parenchyma, there are several passages alternating with the latter; they are numerous in the Narcissus mentioned above, and in Grasses, Cyperaceæ, Sparganium, Typha, Pandanus, and Eryngia; in Lobelia Dortmanna there is one on each side of a median persistent plate.

In tough leaves of Monocotyledons, the more or less complete interruption of the chlorophyll-parenchyma by longitudinal strands of fibrous sclerenchyma, usually containing the longitudinal vascular bundles, is also of frequent occurrence, as will be described in the following chapter; and there are many other special phenomena of alternately dissimilar longitudinal bands, which respectively contain, or are destitute of bundles, e. g. in the leaves of Grasses, large Bromeliaceæ, &c., the detailed description of which in this place would lead us too far.

With regard to the chlorophyll-parenchyma are to be mentioned, as examples of the palisade form, the leaves of the Myrtaceæ mentioned, Proteaceæ, species of Statice, Welwitschia, stem of Casuarina, Salicornia herbacea, Colletia horrida, Scirpus Holoschœnus, lacustris, palustris, Papyrus, Juncus effusus, &c. The leaves of many Monocotyledons, Mesembryanthema, the stems of Bossiæa, Mühlenbeckia platyclados, Cacteæ, Juncus glaucus, &c., may be mentioned as affording examples of the round-celled form.

Cells elongated in the transverse direction, i. e. parallel to the surface, are peculiar to the sword-shaped leaves of many Irideæ, as Iris Germanica, Gladiolus imbricatus, and especially Tritonia deusta. In species of Pinus and Cedrus the cells of the chlorophyll-parenchyma are characterised by the tabular polyhedral form, and the infolding of the walls, mentioned above at p. 118. (See Figs. 11, p. 35, and 27, p. 78.)

2. To the second type belong only flat horizontal leaves, and in fact the majority of them. It is characterised by the fact that the chlorophyll-parenchyma forms the entire substance of the leaf, and is severed into two different layers, each of which corresponds to one surface of the leaf. It may accordingly be termed the *two-sided*, the *bifacial* type. The difference between the two horizontal layers may be generally expressed by the statement, that the one, that namely belonging to the surface which is turned towards the light, is denser than the other, being furnished with less wide interstices, and therefore appearing of a darker green, even when the amount of chlorophyll in each individual cell is the same.

The usual form is such that the denser layer consists, according to the thickness of the leaf, of one or more layers of palisade-cells, the other layer consisting of

[1] Kareltschikoff, *l. c.*; compare p. 118.

many-armed or lamellar cavernous parenchyma (comp. p. 211), which from this spongy character has also been called 'spongy parenchyma.' Yet we often find the cells of both layers of irregular form, and differing only in the size of their protrusions, and of the air-cavities thus produced, e. g. in many leaves of Ferns, as Scolopendrium vulgare, Aspidium falcatum, Filix mas, &c. It is superfluous to mention further examples, but we may refer to the flat foliage-leaves of Dicotyledons and Monocotyledons (Lilium bulbiferum, Aroideæ, &c.), which are dark-green above, and dull-green below.

The dense parenchymatous layer is as a rule less thick than the lacunar one, in many leathery leaves scarcely half as thick, e. g. Malpighia macrophylla. The two are usually sharply marked off one from another, yet there are also cases of quite gradual transition. In the leaves of species of Podocarpus, Cunninghamia sinensis, Sequoia sempervirens, Cephalotaxus, and in many Cycadeæ, as Encephalartos and Zamia integrifolia, the dense, more or less decidedly palisade-like layer is internally bounded by a few layers of loose parenchyma, consisting chiefly of transversely elongated cells containing chlorophyll, which must be distinguished from the transverse elements of the border of tracheides (p. 380)[1].

As mentioned above, the dense parenchymatous layer always corresponds to the surface turned towards the light, the loose layer to the other side. The former is, as a rule, both morphologically and actually the upper surface of the leaf, the latter the lower. These conditions are reversed in the case of the upright leaflets with the edge rolled inwards of Passerina hirsuta[2], filiformis, and ericoides, where lacunar parenchyma lies on the densely hairy concave upper side, and remarkably dense palisade-parenchyma on the convex lower side. A similar relation exists, though in a less marked manner, in the leaves of Juniperus communis and nana[3]. In the flat foliage leaves of Allium ursinum, Alstrœmeria, Geitonoplesium, Eustrephus, and also in many Grasses, the morphologically upper side becomes turned downwards, by torsion of the petiole or of the base of the leaf; this side here has the loose parenchyma, while the side which actually faces upwards has the dense tissue[4].

On the relation of the smaller vascular bundles to the two layers of bifacial leaves, comp. p. 305.

As has already been indicated, intermediate forms between the main types distinguished are not wanting, and among them the greatest variety in detail prevails.

As regards the distribution of the two main types according to the forms of leaves and systematic divisions, no general rule, as far as our present knowledge extends, is to be added to the few that have been adduced above. The principles brought forward that leaves which are not flat and not horizontally placed always have centric chlorophyll-parenchyma, while the latter is bifacial in horizontal and flat leaves only, hold good in this form for all the groups and families which have come under consideration. They cannot however be extended further, nor does the converse hold good, for among flat and horizontal leaves the greatest differences occur in closely related forms, e. g. bifacial structure in Dianthus barbatus, Statice latifolia, Melaleuca hypericifolia, Eucalyptus pulverulenta; Allium ursinum, Epidendron ciliare; centric structure in Dianthus Caryo-

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[1] See Thomas, Pringsheim's Jahrb. IV. p. 37.—Kraus, ibid. pp. 323, 333, &c.

[2] Caruel, in Nuov. Giorn. bot. Italiano, I. p. 194. Already indicated in De Candolle, Organographie, I. p. 274. Compare above, p. 49.

[3] Thomas, *l.c.* p. 39.

[4] Treviranus, Physiol. I. p. 445.—Irmisch, Knollen- und Zwiebelgewächse, p. 4.—A. Braun, Botan. Zeitung. 1870, p. 551.

phyllus and plumarius, Statice purpurea, Melaleuca linearifolia, Eucalyptus Gunnii; Allium nigrum, and the thick-leaved Epiphytic Orchideæ, mentioned above at p. 407.

In addition to the parenchymatous masses described above, there is present in many leaves, and especially in tough ones, a single- or many-layered *Hypoderma*[1], which is, no doubt, always a continuation of the equivalent layer of the stem or petiole. It consists sometimes of elements to be described in the next chapter, sometimes, as in many cases belonging to this category, of thin-walled aqueous parenchyma, the cells of which are in uninterrupted connection with one another and with the epidermis, and in many-layered hypodermata increase in size towards the inside, thus corresponding in all these relations, as well as in the nature of their contents, to the elements of a many-layered epidermis, from which they are only to be distinguished by their origin. Comp. p. 32, and Fig. 44, p. 104. They thus form a strengthening layer to the epidermis. As regards the nature of their walls they often approach the collenchyma, so that in many cases a sharp distinction from the latter is impracticable, and in this respect also they correspond to many epidermal cells. In the leaves of the Pleurothallideæ, mentioned below, their walls have reticulate or spiral thickenings, in Physosiphon, the Bromeliaceæ to be mentioned, and in Æschynanthus the lateral walls vertical to the surface of the leaf are folded, with undulations parallel to the latter.

Many tough Fern-leaves afford examples of this phenomenon, as Polypodium Lingua, Aspidium coriaceum; many Commelineæ, e.g. species of Tradescantia; all Scitamineæ where the point has been investigated, as Musa, Strelitzia (Fig. 29, p. 85), Heliconia, Canna, Costus sp.; many Palms, as Chamærops, Caryota, &c.; many Grasses, e.g. Arundo Donax; many Bromeliaceæ (Bromelia Caratas, Pholidophyllum zonatum, Æchmea, Hechtia, Tillandsia spec.), Orchideæ of the group Pleurothallideæ: Pleurothallis ruscifolia, Lepanthes cochlearifolia, Physosiphon Loddigesii, Octomeria graminifolia, Stelis spec.; species of Pandanus; Aroideæ (Philodendron cannifolium, Anthurium membranuliferum); Æschynanthus spec.; Veronica speciosa, Lindleyana; Stenocarpus sinuatus; Mahonia Fortunei; Quercus glabra; Ilex aquifolium, ovata, and other species; Rosmarinus officinalis, Nerium Oleander, &c. &c.[2]

The hypodermal layers in question consist of one, of several, or of many strata of cells; they are as a rule extended uniformly over the whole surface of the leaf, and only interrupted at the stomata—either by a simple intercellular air-cavity (e.g. Fig. 29, Strelitzia), or by chlorophyll-containing parenchymatous cells surrounding such a cavity. On the upper surface of the leaf they are usually more bulky than on the lower, or they are exclusively present on the former. In many Bromeliaceæ (B. Caratas, Hohenbergia strobilacea), Orchideæ, and Æschynanthus, they there attain a thickness which amounts to $\frac{1}{2}$ or even more than $\frac{2}{3}$ of the entire thickness of the leaf. In the leaves of many Grasses, as Arundo Donax, the thin-celled hypoderma is limited to narrow longitudinal bands, alternating with the vascular bundles, and covered by large, bladder-like epidermal cells; on the upper

[1] Kraus, Cycadeenfiedern, *l.c.*—Pfitzer, Pringsheim's Jahrb. VIII.

[2] Compare Treviranus, Physiol. I. p. 450.—Thomas, Coniferen-blätter, *l.c.*—Kraus, Pfitzer, *l.c.*

side of the lamina of the leaf of Chamærops humilis it is thick, large-celled and many-layered over the main ribs, single-layered and small-celled elsewhere.

Sect. 122. The primary cortical mass of the *root*[1] consists as a rule exclusively or chiefly of parenchyma, the cells of which, corresponding to the original arrangement of the meristem, remain arranged in vertical longitudinal rows. (Compare pp. 9–13.)

In the roots of *Phanerogams* the cortex is more or less sharply severed into two layers, an outer and an inner. The former consists of cells which are usually, though not always, narrower, and are uninterruptedly, or at least very closely, united; in the thicker roots they show, as seen in cross-section, a polyhedral form, are arranged in several concentric, but not in accurately radial rows, and not unfrequently have somewhat thick, collenchymatous walls, which often become sclerotic. In thin roots, e.g. Hordeum, Elodea, Lemna, &c. it is a single hypodermal layer of cells. The inner layer consists in very thin roots, as in those of Lemna minor, of two concentric strata of cells as a minimum, usually of several such strata, while in thick roots they are very numerous. (Fig. 168, p. 360.) The innermost of them is always the endodermis, surrounding the axial bundle. Further, as often mentioned in former paragraphs, the cells of the successive strata are as a rule permanently arranged in radial rows, which are very regular, especially in Monocotyledons. Between their rounded corners they leave spaces containing air, which have the greatest average width in the middle portion of the layer. The larger lacunæ and passages containing air which occur in roots (comp. Sect. 51) belong to the inner layer, or in thick roots to its middle portion. The fibrous thickenings on the walls, described at p. 117, as occurring in Orchideæ and Coniferæ, always belong principally or exclusively to the inner parenchymatous layer of the root.

The successive concentric strata of cells of the inner layer arise, with few exceptions, from the initial cells by tangential divisions in centripetal order, in Acorus Calamus and other Aroids centrifugally; in several cases (Zea, Helianthus, Palms) the later tangential divisions appear in less regular succession. Where the whole cortex proceeds from a single initial layer, the first tangential division of the latter (leaving the epidermis out of consideration) seems always to cut off the outer layer, which then either remains undivided, or undergoes a few further tangential divisions, which in Stratiotes take place in strictly centrifugal succession. In Linum (p. 12) a special initial layer for the single external layer of the cortex extends round the meristematic apex. In the type of root described at p. 12, with a transverse common initial zone at the growing-point, the succession of the tangential divisions likewise appears not to be quite regular.

The single layer of cells bordering on the epidermis, which, as already stated above, is often distinguished by a special structure, and always by uninterrupted lateral connection of its cells, is named *endodermis* by Nicolai. As in the present work this word has been used for layers of cells which, without reference to the *place* of their occurrence, are characterised by a definite structure, this term cannot be maintained. According to its position and origin, this layer, which in agreement with the terminology here constantly

[1] Compare the works of Nicolai, Nägeli and Leitgeb, Van Tieghem, Janczewski, &c., which are cited at pp. 7, 351, 356.—Reinke, in Hanstein's Botan. Abhandl., Heft 3. [Also, Olivier, Recherches sur l'appareil tégumentaire des Racines. Ann. Sci. Nat. Sér. 6, Tom. 11, 1881.]

used is to be called the *hypodermal* layer, is in most cases equivalent to the outer endodermis of the aerial roots of orchids (pp. 125 and 227). Its structure also appears in many roots to be actually that characteristic of the endodermis, as in Elodea according to Nicolai, and also in Acorus Calamus, so that the occurrence of a hypodermal endodermis would thus have a wider distribution than was stated above. Further investigations of this point are to be undertaken, for the existing data do not appear to me to afford sufficient certainty. The roots of Orchideæ investigated also have a denser, smaller-celled parenchymatous layer below their endodermis, and in the case of most roots the endodermal structure of the hypodermal layer is at least very doubtful.

Corresponding to the conformity prevailing in the other conditions, and apart from differences in the first origination, and in the phenomena of sclerosis to be described later, the structure of the cortex of the root in *Filices*, *Hydropterideæ* and *Equiseta*, is similar to that in the Phanerogams. In every sextant of the apical meristem (p. 18) the initial cell of the periblem, which after severance of the plerome-cylinder and the epidermis remains between the two, is divided by a tangential wall into an outer cell which is the initial cell of the outer cortical layer, and an inner initial cell of the inner cortical layer; the former increases the number of concentric layers by tangential divisions advancing chiefly in centrifugal direction, the latter by those advancing in centripetal direction; the number of members of each layer increases by radial divisions. In the Filices and Hydropterideæ it is the innermost layer of cells, in the Equiseta it is the second layer from inside which becomes converted into the endodermis. In thin roots the tangential divisions are not very numerous, the radial ones in many cases are even wholly omitted in the inner cortical layer, so that the axial bundle, as seen in cross-section, is only surrounded by six endodermal cells, the latter by the same number of cortical cells, which are relatively very large. (Fig. 169, p. 363.)

A noticeable phenomenon, which is apparently of frequent occurrence among the Polypodiaceæ and Osmundaceæ, is that the entire cortex soon begins to show dark brown membranes, and uninterrupted connection between them, although the cells do not cease to contain starch, a condition which, however, is by no means common to all Ferns, e. g. it is absent in Scolopendrium, Ophioglossum, Marattiaceæ, &c. The species of Isoetes and Selaginella and the Lycopodiaceæ agree in the main with the forms described, as regards the conditions here under consideration. For details and the history of development we may refer to the special works cited.

The *root cap* always consists of parenchymatous cells, which in the younger stages contain abundant starch, and are uninterruptedly connected one with another. In old age they die off, as is well known, successively, in many cases after breaking up into layers or rows (exfoliation), a phenomenon which has its anatomical basis in the fact that the limiting layers of the walls become disorganised to an amorphous mucilage. In most roots the number of the successive layers of the cap is large, and the layers as they peel off are constantly replaced by renewed ones, the end of the cap having the conical form represented above, pp. 9 and 12. In other cases the renewal of the layers soon ceases; e. g. according to Caspary and Nicolai in the Nymphæaceæ, Æsculus, Najas, Lemna, Hydrilla, and Hyacinthus; and according to Janczewski in Pistia and Hydrocharis. In the Nymphæaceæ, except Nuphar, the cap is persistent, in the other cases mentioned, especially in the thinner, few-layered caps of the water-plants mentioned, the layers successively die and peel off. The main root of

Trapa natans has no cap, although, according to Reinke, it shows at least an indication of one in the form of isolated tangential divisions of the epidermal cells.

Sect. 123. As often had to be mentioned in former sections, the limiting layers, where parenchymatous masses adjoin non-equivalent groups of tissue, are often developed in the form of distinct layers, which stand to the latter in the relation of *sheaths*. The hypodermal layers of foliage-leaves already described, as well as the limiting layers between the sharply-bounded central portion and the chlorophyll-parenchyma of centrically constructed leaves, belong essentially to this category (comp. Fig. 185, p. 381). But the endodermis of many aërial roots, already considered in Sects. 27 and 56, and the parenchymatous sheaths, which stand in immediate relation to the vascular bundles or to definite groups of them, still require to be especially mentioned here. According as the one or the other of these latter relations exists, and thus, according to their position, we have first to distinguish those parenchymatous masses, each of which surrounds one vascular bundle,—and then frequently also the fibrous strand which may accompany it;—and secondly others, which mark off the bundle-ring or cylinder from the surrounding tissue. The designation of the two forms distinguished according to their position, follows obviously. Inasmuch as in roots and stems, the axial vascular bundle, or the bundle-ring or cylinder, corresponds to the primary plerome, while the surrounding parenchymatous sheath answers to the innermost layer of the periblem, the name *plerome-sheath*[1] is appropriate for the latter, even in cases possibly occurring in which the name chosen according to the primary differentiation of the meristem may not apply quite exactly.

An internal sheath, occurring on the side of the bundle-ring next to the pith, exists only in some species of Equisetum, mentioned at p. 122.

The plerome-sheath of the stems of Phanerogams also lies outside the fibrous strands accompanying the peripheral bundles of the cylinder, where such strands are present. According to Van Tieghem[2] it is always separated from these or from the phloem-portions of the vascular bundles by a single or few-layered zone of parenchyma, and this forms the continuation of the pericambium of the main root, while the plerome-sheath itself is continued directly from the latter into the stem.

Sheaths of the plerome and ring, as well as those of single vascular bundles, appear in two principal forms, namely in the form of the *endodermis*, or in that of a single layer of cells, which agrees with the endodermis in the close lateral connection of its elements, but is destitute of the characteristic structure of its walls, being only distinguished from the surrounding tissue by less conspicuous differences of cell-form, and by permanently containing abundant small starch-grains. From its latter characteristic it has been called the *starch-layer* by Sachs. That the endodermis is also often distinguished by containing abundant starch, was already stated at p. 125. Other peculiarities of the cell-contents, as abundant tannin, characteristic pigments, &c., also frequently occur in both cases. Apart from the close relation between the starch-ring and the endodermis already indicated by the above statements, forms occur as to which it is doubtful whether the one or the other term is appropriate, and which are thus intermediate, e. g. the plerome-sheath in the stem of

[1] Sachs, Textbook, p. 124, 2nd English edition.
[2] Ann. Sci. Nat. 5 sér. tom. 16, p. 112.

Lactuca virosa, and the bundle-sheath in the stem of Ranunculus fluitans; comp. the explanation of Fig. 153, p. 332. The two forms of sheath may mutually replace one another in the same region, according to the species; the plerome-sheath, for example, appears in the hypocotyledonary stem of Helianthus annuus as a starch-layer, in that of Tagetes patula as an exquisite endodermis. The thin vascular bundles, especially the bundle-ends of the foliar expansions, are usually surrounded by a parenchymatous sheath different from the two distinguished above, and consisting of elongated elements passing over gradually into the epithema at the peripheral ends. (Comp. Sect. 111.)

The sheath of single trunks of vascular bundles appears in the form of an *endodermis*, around the axial bundles of roots and of most stems which have them, around the bundles of almost all Ferns, and those in the stem and leaves of certain Phanerogamic plants. To the cases and descriptions already given in Sect. 27, and Chap. VIII, we have here to add the bundles of the leaves of Hottonia, Cortusa, Dodecatheon, Cyclamen, Soldanella, Trientalis[1]; those of the stem of Caltha palustris, which, according to Russow, are surrounded by a wholly or partially sclerotic endodermis; and especially, according to the statements of the latter author[2], and of Schwendener[3], the bundle-trunks in the leaves of Cyperaceæ, Juncaceæ, and Grasses, in which the endodermis, which usually soon becomes thickened by sclerosis, lies between the vascular bundle and the strand of sclerenchyma ensheathing it.

An endodermis ensheathing the whole ring of bundles is present both on the cortical and the medullary side of the latter, in the species of Equisetum enumerated at p. 122. In other species of this genus, e. g. E. palustre, Fig. 149, p. 329, it only extends around the cortical side of the ring of bundles, and the same is the case with the endodermal plerome-sheath which surrounds the ring or cylinder of the stems of Phanerogams. As selected examples for the occurrence of this, have already been mentioned (p. 121) the stems of Cobæa, Tagetes, Lobelia spec., the rhizomes of Scitamineæ, Cyperaceæ, &c. According to the investigations of Dr. v. Kamienski, which have been privately communicated to me, numerous Dicotyledons are to be added to this list; Linaria, Pedicularis spec., Camelina, Capsella, Atriplex patula, Euphorbia spec., Mercurialis, all Primulaceæ; and according to Vöchting[4] the Melastomaceæ. Further investigations will have to decide how far the endodermal structure of the layer surrounding the plerome and vascular bundles in stems and leaves generally is of usual occurrence.

The plerome-sheath is developed in the form of the *starch-ring* or *starch-layer*[5] in the stem of most Dicotyledons, as far as can be decided from the existing investigations. Sachs, for example, finds this to be the case in seedlings, especially in the hypocotyledonary stem of Helianthus annuus, Cucurbita, Phaseolus, Iberis, Raphanus, Prunus, Amygdalus, Convolvulus, Quercus, Acer, Ricinus, (comp. Fig. 154, p. 333), in the stolons of the potato, and in the mature stem of Dahlia and Ricinus. The starch-layer is in these cases either uniformly developed around the whole ring of bundles,

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[1] Kamienski, private communication.
[2] Vergl. Unters. pp. 169, 170.
[3] Das mechan. System, p. 17.
[4] *l. c.*; compare p. 259.
[5] Sachs, Botan. Zeitg. 1859, p. 177, Taf. VIII. IX; Pringsheim's Jahrb. III. p. 194.

e. g. Fig. 154, or it only contains starch opposite the vascular bundles; e. g. in the stem of Brassica oleracea; or only opposite the medullary rays of the ring (shoots of Atragene alpina). In the latter cases, the layer, in so far as it contains no starch grains, is difficult to distinguish.

A sheath developed as a starch-layer is present around the single bundle-trunks, and then also embraces the accompanying fibrous strand, in the leaves of Dicotyledons, and in the stem and sheath of the leaf of Monocotyledons (e. g. Grasses, as Triticum, Zea). In the former cases it embraces the outer edge of the bundle, in the Monocotyledons the inner (comp. Fig. 151, p. 331).

As regards the sheaths of the ultimate ramifications and ends of the vascular bundles, the latter, as already stated in Sect. 111, are surrounded in the foliar expansions of Angiospermous plants by a layer of parenchymatous cells elongated in the direction of the course of the bundle; these cells are closely attached to the bundle, and are laterally connected one with another without interruption. Their surfaces remote from the bundle often border on the air-containing interstices of the surrounding parenchyma, and where they abut on many-armed lacunar tissue their walls are often folded like those of the latter. In many leaves they resemble the surrounding cells in containing abundant chlorophyll, e. g. Fuchsia, Papaver, Primula sinensis, Zea, and Triticum (comp. Figs. 173, 175, 178, pp. 372–375); in thick leaves they often contain little or no chlorophyll.

CHAPTER X.

ARRANGEMENT OF THE SCLERENCHYMA AND SCLEROTIC CELLS.

Sect. 124. As shown by their anatomical characteristics, and as Schwendener has demonstrated, sclerenchyma and sclerotic cells form the strengthening apparatus of the plant; the former is specifically and almost exclusively adapted to the mechanical function mentioned, the latter serves other functions simultaneously in different degrees; the two are connected one with another by various transitional forms. Accordingly they may both bear a common name, viz. stereides, or sterenchyma; and the groups they form may with Schwendener be termed stereome. The collenchymatous masses also are immediately related to the sterenchyma as transitory strengthening apparatus which often passes over into sclerenchyma, and hence we must often take them into consideration in treating of the latter. The same applies to sclerotic endodermal layers, which have been discussed in former chapters.

Schwendener, in his excellent work which has been so often mentioned[1], has treated both the arrangement of the sclerenchymatous masses and their physiological relations so minutely and comprehensively, that any detailed exposition of the former, within the space here available, must be a mere extract from his work, or must seem like one. I therefore think it best to refer once for all to the book mentioned, merely giving short indications respecting the masses of sterenchyma which serve to strengthen entire organs, as stems, petioles, &c., and only entering more minutely into some of the points which have received less attention in Schwendener's work.

In the vegetative organs of the Phanerogams, to which, among the groups of Filicineæ, the Equiseta and the non-aquatic species of Isoëtes are in this respect especially related, the sclerenchyma is usually more sharply differentiated throughout than in the majority of the Ferns. The latter may therefore be treated subsequently by themselves, and for the present be left out of consideration.

Sect. 125. **Sclerenchymatous fibres**, or **sclerotic elongated cells** which approach them very nearly, occur generally in parts which are exposed to bending or tension, and are united to form *strands*, *layers*, or *sheaths*, which traverse the entire organ longitudinally.

As regards their arrangement, we find in the first place strands and layers in the hypodermal region, partly in direct contact with the epidermis, partly separated from it only by one or a few layers of cells. It is a phenomenon of wide occurrence

[1] Das mechanische Princip, &c., Leipzig, 1874. [See also Haberlandt, Entwickelungsgeschichte des mechanischen Systems; 1879.—Westermaier, Z. Kenntniss des Mechan. Gewebesystems; Bot. Ztg. 1882, p. 174.]

that both in angular and round stems and petioles longitudinal hypodermal bands of fibres are found alternating with chlorophyll-parenchyma; the former project toward the inside in a more or less convex form or as a strong ridge. This is the case in numerous 'halms' of Cyperaceæ, species of Juncus, and Panicum turgidum. In angular or channelled stems of Dicotyledons, the corresponding longitudinal bands are usually collenchymatous; they become sclerenchymatous in many Umbelliferæ (Chærophyllum bulbosum), Papilionaceæ (Spartium monospermum), and the Casuarinæ; further in Ephedra and the Equiseta[1]. The same phenomena appear in very wide distribution in tough hard leaves. Thick hypodermal ridges of sclerenchyma, often projecting deeply inwards, traverse the lamina in Cyperaceæ, Typha, Sparganium, Dasylirion, Phormium, Palms, &c.[2]; in conjunction with the vascular bundles inserted in them, to be mentioned again below, they often form in flat leaves vertical plates passing through from one surface to the other. Similar conditions are shown by the ribs of many tough Dicotyledonous leaves, as a fibrous bundle projects into them from one or both sides, upon or between which the vascular bundles are attached, e. g. Eriobotrya japonica, Theophrasta ornata, Laurus, Passerina filiformis, Rosmarinus, and many others. Here also intermediate forms between collenchyma and sclerenchyma frequently occur. Numerous plates of sclerenchymatous fibres projecting deeply inwards on both sides traverse the leaf of Welwitschia (Fig. 187, p. 408). In the leaves of the terrestrial species of Isoetes[3] a hypodermal strand of fibres passes along the anterior and posterior surface of the middle line, and in each of the two marginal angles; between these four, additional smaller ones may appear according to the species.

In most stems and leaves the fibrous strands are sharply limited laterally towards the heterogeneous bands alternating with them, quite up to the epidermis. In other cases they are connected with one another by means of a continuous hypodermal fibrous layer consisting of a few strata, into which their lateral edges are extended, and this layer follows the entire inner surface of the epidermis, and is only interrupted at the stomata, e. g. stem of Equisetum hiemale, and Casuarina.

To the latter arrangement are related the hypodermal fibrous layers, often present in tough leathery leaves, which, with an average thickness of a few strata of cells, run with approximate uniformity around the entire surface, becoming thicker at the edges and angles, but constantly interrupted at the stomata, and rarely by small gaps at other places. Such fibrous layers[4] occur in numerous tough leaves of Bromeliaceæ[5] (Ananassa, Bilbergia zebrina, Bromelia Caratas, &c.); in the leaves of certain Orchids (Vanda furva, Renanthera coccinea); in the pinnæ of many Cycadeæ, e.g. Cycas, Encephalartos, extending sometimes all round, sometimes only on the upper side; and in most leathery leaves of Conifers[6] (Fig. 183, p. 380; Fig. 185, p. 381; and

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[1] Compare Pfitzer, in Pringsheim's Jahrb. VIII. p. 60.—Mettenius, Hymenophyllaceæ, p. 439.—Jochmann, Umbelliferarum structura, p. 8.

[2] Compare Pfitzer, *l. c.*—Mohl, Palm. struct. Tab. K, L.—Karsten, Veget. Org. d. Palmen.

[3] A. Braun, Monatsber. d. Berlin. Acad. 1863, p. 588.

[4] Cf. Pfitzer, *l. c.*

[5] Mohl, Verm. Schriften, p. 265, Taf. X.

[6] Compare Kraus, Cycadeenfiedern, *l. c.*—Von Mohl, Botan. Zeitg. 1871, p. 7.—Thomas, in Pringsheim's Jahrb. *l. c.*

Fig. 27, p. 78). They form a thick uninterrupted layer on the upper side of the leaf of Jacquinia ruscifolia, an often interrupted layer on the lower side of this leaf, and on both sides of that of Theophrasta ornata and species of Olea. This form of the strengthening apparatus is absent, however, in most leathery leaves, and in fact this is the case even in such species as are closely related and similar to those mentioned, e. g. most leathery leaves of Orchids, Pholidophyllum zonatum, Zamia integrifolia, Taxus, Cephalotaxus spec., Tsuga Canadensis, Abies amabilis, &c.

. A continuous two- or many-layered fibrous investment further appears in the aerial roots of Philodendron Imbe, Rudgeanum, and other species[1]. In the Cyperaceæ, e. g. species of Carex, the outer layer of the cortex of the root is often sclerotic in a high degree, and throughout many strata of cells.

The second form of distribution of sclerenchymatous masses is that in which they lie at a greater distance from the epidermis, in the inner regions, being united so as to form either a continuous annular layer or isolated strands.

The former arrangement occurs in a number of stems, in such a form that the fibrous ring lies in the external cortex, bordering within and without on parenchymatous layers: shoots of Berberis vulgaris; Caryophylleæ, as Dianthus plumarius, Gypsophila altissima, Silene Italica; Cucurbitaceæ; and climbing Aristolochiæ, as A. Sipho[2]. Usually, however, the fibrous layer lies on the outer border of the bundle-ring or cylinder, in such a manner that it includes the vascular bundles, or in the latter case the outermost of them, or that they rest against it. In this case, and in Berberis[3], and doubtless also in the other plants mentioned with it, the ring belongs, according to its origin, to the outer layer of the plerome, it marks, more or less sharply, the outer *boundary of the plerome*. This phenomenon is of most frequent occurrence in Monocotyledonous stems. It occurs in the halm of many Grasses and of many Cyperaceæ and Juncaceæ, and in fact sometimes in combination with the occurrence of hypodermal fibrous ridges, which, as processes of the ring, unite the latter with the epidermis, e. g. Piptatherum, Molinia, Bromus spec.[4]; or penetrate from the outside close up to the ring without reaching it (Alopecurus pratensis, Panicum turgidum, Juncus paniculatus); or, lastly, show sometimes one, sometimes the other condition (Cladium Mariscus). Other plants belonging to the families mentioned show the sclerenchymatous ring connected only with isolated ridges of the epidermis, or without this connection, and only with projecting ribs, which correspond to the insertion of vascular bundles, on its outside; e. g. Rhynchospora alba, Juncus bufonius, Pennisetum longistylum. To the latter cases is related the smooth and sharply limited sclerotic ring, which, with numerous individual modifications, forms the outer boundary of the cylinder, and includes or supports the peripheral vascular bundles in most Monocotyledonous foliage-stems: Restiaceæ, Eriocauloneæ partly, Commelineæ, Melanthaceæ, Liliaceæ, Smilaceæ, Tamus, Irideæ, Orchideæ, Alismaceæ, Typhaceæ, &c.; and in most rhizomes, also belonging to the families mentioned above.

The same phenomenon of a sclerenchymatous ring directly supporting or

[1] Van Tieghem, Struct. des Aroidées, *l. c.*

[2] Compare Treviranus, Physiol. I. p. 209.—Caspary, Pringsheim's Jahrb. I. p. 444.—Sanio, Botan. Zeitg. 1864, p. 222.—Von Mohl, Palm. Struct. Tab. H.—Mettenius, *l. c.*

[3] Compare Schmitz, *l. c.* (p. 393).

[4] Compare Schwendener, *l. c.*

including the bundles, recurs in numerous Dicotyledonous stems: Caryophylleæ, e.g. Silene catholica, Saurureæ, Podophyllum, species of Thalictrum (also in the petiole), Papaver, Plantago, Trientalis, Hypochæris radicata, &c.[1]

The converse case, that a continuous layer of sclerenchyma supports the whole inner side of the ring of vascular bundles, is rare in Dicotyledonous stems. This is the case in woody Piperaceæ—Artanthe, Chavica spec.[2], and is especially characteristic in the shoots of Bougainvillea spectabilis.

In tough firm organs, longitudinal fibrous strands, which are not distributed in the hypoderma, and which in the whole or a part of their course stand in no direct relation to the vascular bundles, are more frequent than continuous annular layers. Examples of this are afforded by the cylindrical or prismatic strands in the parenchyma of the leaf and petiole of Marantaceæ, Palms, Dracænæ, and Pandanus, which, as regards their position, are connected with the hypodermal strands by various transitional forms; e.g. the strands in the interior of the leaf of Welwitschia (Fig. 187), and in the cortical parenchyma of Ephedra, the strands in the internodes of many Potamogetons, mentioned at pp. 232 and 271, and represented in Fig. 171, p. 369; the little bundles occurring in the parenchyma of the stem-cylinder of many Palms (Astrocaryum, Cocos, Leopoldinia, Lepidocaryum spec.[3]) between the vascular bundles and those which traverse the cortex of most Palm-stems; the numerous strands in the rhizome of Acorus[4], in the cortex of the root of Phœnix, Cocos spec.[5], and of the Pandaneæ, and in the axial cylinder of thick roots of the same (comp. p. 361) and of the Iriarteæ.

In many of the cases mentioned, the fibrous strands have an isolated course, without connection with the fibres accompanying the vascular bundles; e. g. in the roots mentioned, in Ephedra and Welwitschia; also in the leaves of Dracæna, as far as my experience goes.

The leaf of D. reflexa[6], as seen with the naked eye, is traversed longitudinally by more than thirty nerves, of which about eighteen are stronger and darker, anastomosing here and there by means of fine transverse branchlets; these are the vascular bundles lying in the middle lamella of the leaf (comp. p. 320), and paler nerves alternate with them. The latter are simple small bundles of fibres. They do not lie in the middle lamella of the leaf, but below the two surfaces, separated from the epidermis by one or two layers of chlorophyll-parenchyma. In the interval between two vascular bundles they usually lie 3–5 together (next the edge 1–0), so that the total number amounts to nearly fifty, which cannot all be clearly distinguished with the naked eye. The smallest are only 5–7 fibres thick, the strongest contain about three times that number. The bundles taper off gradually and terminate below the apex of the leaf, and immediately above its base, and do not anastomose. Nor did I see them enter the cortex of the stem. In the case of other fibrous bundles, the anatomical relation to the sheaths of the vascular bundles still needs investigation. As regards those of

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[1] Compare Schwendener, *l. c.*, p. 143, and the references in the notes, pp. 248–250.
[2] Sanio, Botan. Zeitg. 1864, p. 214.
[3] Von Mohl, Palm. Structura; Verm. Schriften, pp. 155, 170.
[4] Van Tieghem, Struct. des Aroidées, *l. c.*
[5] Von Mohl, Palm. Struct. p. xx.
[6] The determination of the species not quite certain.

the Potamogetons it has already been stated (p. 232) that they anastomose in the node with one another and with the vascular bundles. Those in the cortex of Palms, as already described at p. 266, after running through many internodes, are sometimes prolonged into purely fibrous bundles, which pass out into the leaves, and sometimes pass over into the fibrous investment of vascular bundles, which likewise make their exit into leaves. Connected with this is the phenomenon likewise mentioned above, of the occurrence, in the plants last named, of intermediate forms between purely fibrous strands and those which contain small complete vascular bundles or single sieve-tubes.

It may here be the best place to recall to mind the fibrous strands which surround a secretory passage in the leaves of Pinus and the roots of Philodendron. Comp. p. 202, Fig. 185, p. 381; Fig. 168, p. 360.

The phenomena hitherto described show that the arrangement of fibrous strands and fibrous sheaths is in a high degree independent of the course of the vascular bundles; but that, on the other hand, there are also close relations between the two. A further phenomenon, corresponding to the attachment of the vascular bundles in stems to the rings or sheaths described, or their inclusion in the latter, occurs widely, especially in the Monocotyledons mentioned above, inasmuch as the vascular bundles are attached to the inner edge of the hypodermal fibrous ridges which project inwards, or are included in the latter. In flat leaves with fibrous ridges passing vertically through them from one side to the other, the latter often have a bundle inserted in the middle, or several one above another near the middle. Side by side with these, other ridges or strands often occur, at least among Monocotyledons, which are quite similar to the former in structure, but contain no vascular bundles, whether they are so far related to one of the latter that they stand opposite to it, or whether even this relation is absent.

In so far as the vascular bundles are attached to or included in those of the sclerenchyma, the latter stand to the former in the relation of *sheaths*. The same relation, as already stated above (Sect. 99 et sq.), is also of general occurrence in the case of those vascular bundles which are not attached to continuous sclerenchymatous sheaths or to hypodermal strands; the sclerenchymatous fibres follow their course as bundle-sheaths (p. 318), which may serve both as a local protective apparatus for the single bundle, and as a strengthening apparatus for the entire organ. Together with the vascular bundles they form *fibrovascular bundles* (p. 318). Sclerotic endodermis may take part in this function, as was stated in former paragraphs. Between sheaths which simply follow the bundle, and attachment to sclerenchymatous bundles the position of which is otherwise determined, the most various intermediate forms occur, as shown in detail by Schwendener.

Apart from these relations of position, the fibrous sheath of the bundle is either *closed all round*, or *partly interrupted*, or only *partial*, i. e. limited to a relatively small portion of the circumference. The first-mentioned relation of complete sheathing obviously occurs in those of the cases above-mentioned, where the bundles are completely inserted in a closed ring of sclerenchyma. It further exists in other forms of insertion or attachment, and in the case of individual fibro-vascular bundles, especially, but not exclusively, in Monocotyledons. In isolated collateral fibro-vascular bundles the fibrous sheath is then rarely of approximately equal thickness

all round, e. g. in the rhizome of Carices. In the majority of cases it is thicker on the outside, where it embraces the phloem, than on the inner border of the bundle; the converse relation occurs more rarely, e. g. in the rhizome of Scirpus palustris, in the periphery of the stem of Saccharum officinarum, Bambusa spec., and other species described by Schwendener. And further its thickness usually diminishes at the lateral edges of the bundle, so that here, especially next the limiting surface of xylem and phloem, it is often only 1–2 layers of fibres in thickness, while at the outer or inner edge its thickness amounts to many layers. This is the case, for example, in most bundles of Acorus and Zea (comp. Fig. 147, p. 317; Fig. 150, p. 330), and many other Monocotyledons; in the stem of Saururus and its allies, in the leathery leaves of species of Melaleuca, Eucalyptus, Eugenia, Callistemon, &c.

To the latter condition is related the most frequent form of local *interruption* of the fibrous sheath, which consists in the presence of a gap of greater or less extent, filled up by comparatively thin-walled parenchyma, next the lateral edges of the limiting surface of phloem and xylem. Such gaps, or 'avenues' as Schwendener calls them, from the surrounding parenchyma to the vascular bundle, are a widely distributed phenomenon in the region indicated, among the bundles of tough parts of Monocotyledons, e. g. in the stem of Canna, the leaves of Typha, Musa, Yucca, and Phormium spec. The bundle of Ranunculus repens represented in Fig. 152, p. 331, is a good example of this, as is also that of Welwitschia, Fig. 157, p. 335; the same condition obtains in the bundles of many tough Dicotyledonous leaves, e. g. species of Hakea and Lomatia. Lateral avenues also appear to occur occasionally in the leaves of the Myrtaceæ mentioned above.

In a species of Bambusa investigated by Schwendener, an avenue exists on the inner side of the internal bundles of the stem, in addition to the two lateral ones. The fibrous strand, which is of immense thickness on the inner edge, is here divided by a transverse lamella of parenchyma into a narrow, thicker-walled section bordering directly on the xylem, and a broader, thinner-walled peripheral section. The former is usually interrupted by two short bands of parenchyma, which lead from the transverse lamella to the xylem.

The *partial fibrous sheath* of collateral vascular bundles usually occurs in such a form that the phloem is supported in its whole extent, or only at its outer edge, by a more or less strongly developed fibrous mass, often only by a small group, or even by single scattered fibres. This is the prevailing rule in the leaves and stems of Dicotyledons (Figs. 154, 156, pp. 333 and 334), and is besides not uncommon in Monocotyledons, e. g. in the leaf of species of Crocus, Agave, and Dracæna, in the sheath of the leaf of Zea (Fig. 151, p. 331), and in the stem and petiole of Aroideæ, as Arum and Colocasia. Comp. also the small bundles of Acorus, Fig. 147, p. 317.

The converse condition, that the partial fibrous sheath embraces the inner edge of the xylem, is more rare: it occurs in the smaller bundles in the periphery of the halm of Papyrus, the halm of Cyperus vegetus and other Cyperaceæ (comp. Schwendener, *l. c.*).

The fibrous strands which appear in company with the vascular bundles often occur, as shown by the examples of Grasses and Cyperaceæ adduced above, side by side with those otherwise arranged, but in very many cases they are present alone. The latter holds good for most of the Dicotyledons which are not expressly

mentioned above as examples of the contrary. Among the tough stems of Monocotyledons, the Bambuseæ investigated show the same behaviour. In many stems of Monocotyledons the sclerenchymatous strands occur chiefly, though not exclusively, in company with the vascular bundles; this is the case in the thick stems of Zea, Saccharum, &c., Palms, and Pandaneæ; also in the stems and petioles of Aroideæ, as Colocasia, Arum, and many others. It is the rule in Monocotyledonous stems, and petioles resembling them in structure, that both the relative and absolute thickness of the strands accompanying the vascular bundles, as well as the thickness of the walls of their elements, increase as they approach nearer to the periphery of the bundle-cylinder. In the Aroideæ mentioned, the bundles, with the exception of the outermost circles, are without a fibrous covering. In most Palm stems, the periphery of the bundle-cylinder, which is surrounded by a narrow cortex, is formed of massive fibrous bundles, separated by narrow bands of parenchyma; on the inner side of each of them a small vascular bundle is attached or inserted; this region therefore consists chiefly of firm masses of sclerenchyma, while the bundles in the interior of the stem, as follows from their general course (p. 262), stand farther apart, and have in every respect a weaker fibrous investment.

Finally, it scarcely needs to be especially stated, that in the case of vascular bundles which are accompanied by fibrous strands and which gradually become longitudinally united a union of the fibrous strands also takes place. If the latter happens earlier than the union of the vascular bundles themselves, the latter, as seen in cross-section, appear inserted, two or more together, in one fibrous strand, as is conspicuously evident in the periphery of Palm-stems, and especially in the stems of the Pandaneæ.

Lastly, we must here once more call attention to the fact that the fibrous strands are often derived from collenchymatous elements. Those strands, or those sections of them, which belong to parts characterised by long-continued capacity for growth and curvatures due to growth, show collenchymatous properties as long as this capacity is maintained, or they show an intermediate character between sclerenchyma and collenchyma; e. g. the base of the sheaths of leaves in the Grasses (Fig. 151), and the above-mentioned stems of Aroideæ.

Sect. 126. In certain relatively rare cases, isolated sclerenchymatous fibres, or fibres united through part of their course to form small bundles, occur in the parenchyma, external to, and usually side by side with, the strands and layers described. To this category belong, in the first place, those branched elements projecting into the air-spaces, which under the name of internal hairs have already been minutely described above (Sect. 53, p. 221) in the case of the Nymphæaceæ, Limnanthemum, Rhizophoreæ, and many Aroideæ. Elements more or less similar to those mentioned occur elsewhere fixed in dense parenchyma. As isolated cases of this sort may shortly be mentioned the unbranched fibres in the cortex of the root of Chamædorea elegans, already dealt with at p. 129; also the branched fibres in the pith of Carissa arduina[1], and the often branched fibres, 6–14^{mm} in length, which Trécul[2] found in the cortex of Euphorbia rhipsaloides, and in the pith and cortex of E. xylophylloides.

[1] A. Gris, *l. c.*, compare p. 403. [2] Comptes Rendus, LX. p. 1349.

Isolated fibres, sometimes ramified, sometimes unbranched, occur as a widely distributed and characteristic phenomenon in the parenchyma of the cortex and leaves of many Gymnosperms, and to this mode of occurrence, as well as to that described in the case of the Nymphæaceæ and Aroideæ, their appearance in a number of tough Dicotyledonous leaves is related.

Many of the phenomena belonging to this category, and the literature referring to them, have already been mentioned in Sect. 30 (p. 130), to which reference must therefore be made.

Among the Gymnosperms, many *Cycadeæ* (Dion, Ceratozamia, Encephalartos, &c.), and several *Coniferæ* (e. g. Cunninghamia, Fig. 183, p. 380), show longitudinal unbranched fibres, occurring isolated or in small groups, in the parenchyma of the petiole and leaf. The same applies to the cortex of Ephedra. Stellately-branched fibres lie scattered in the chlorophyll-parenchyma in Sciadopitys, Dammara, and Araucaria imbricata. The latter recall the fibres, differing from those of the hypoderma, by which the entire parenchyma of Welwitschia, even including that of the floral organs, is abundantly permeated, the resemblance consisting especially in the presence of great numbers of crystals of calcium oxalate deposited on their surface: they are thick and short spindle-shaped elements, with short protruding branches here and there at their pointed ends, and with a very thick, much stratified, lignified wall (comp. Fig. 55, p. 132, and Fig. 187, p. 408). In the stem these fibres are directed without order towards different sides. In the leaves, where they are on the average somewhat narrower than those of the stem, they lie as a rule, not without exception, in the middle lamella, parallel to the surface of the leaf, with their longitudinal axis sometimes directed longitudinally, sometimes transversely or obliquely with reference to that of the leaf; they usually stand about at right angles to the surface of the leaf, on both sides of the middle lamella, in the chlorophyll tissue traversed by fibrous bundles; they reach the middle lamella with one end, and the inner surface of the epidermis with the other, and often have a hook-like bend at the latter, or are even wedged in between the inner parts of the epidermal cells. In the parenchyma of the third genus of Gnetaceæ, *Gnetum*, at least in the species investigated, sclerenchymatous fibrous cells are no less abundant than in Ephedra and Welwitschia; in Gnetum Gnemon they are present in the entire parenchyma of the external cortex, here running longitudinally, and branching rarely or not at all, also in the pith of the nodes, and in the leaves near their surfaces, especially the upper, to which they are nearly parallel; in Gnetum Thoa they occur in the same way in the outer cortex, but especially in the pith of the nodes and in the leaves; in the regions last mentioned they are abundantly and variously ramified, in the leaf their size is very unequal, sometimes very considerable. Comp. p. 130.

The leathery leaves of all these Gymnosperms are thus strengthened by a complicated sclerenchymatous frame-work. Among Dicotyledons the leaves of Camellia and Fagræa are characterised by numerous fibres scattered in the parenchyma, which are abundantly and irregularly branched (Fig. 53, p. 130); this also applies to the leaf of species of Olea. In Olea europæa the fibres are very irregular in their ramification and direction, sending out branches on all sides as far as the under surface of the epidermis; in O. fragrans 'they extend, usually without branching, right across the whole leaf at right angles to the surface, and branch in a more or less pedate manner at the upper and lower epidermis, so that they act as columns, connecting the two epidermal layers together.' (Thomas.) In the Proteaceæ mentioned at p. 130, rod-shaped, more or less ramified sclerenchymatous fibres stand between the palisade-like chlorophyll-cells, at right angles to the inner surface of the epidermis. They are as high as, or somewhat higher than the parenchymatous layer on either side which contains the chlorophyll, and with their usually branched ends they adhere on one side to the epidermis, while on the other they are attached to or wedged into the middle layer of the leaf, which in the thick-leaved species is destitute of

chlorophyll. Still stouter, shortly-branched fibrous cells stand in the palisade-parenchyma on either side of the leaves of Statice purpurea, approximately at right angles to the surface, but without reaching the epidermis.

Sect. 127. Short sclerenchymatous elements occasionally appear in the primary structure of the Phanerogams, united, like the fibres, to form hypodermal strands or sheaths, or as portions of them. This is the case with the hypodermal layers in Palm-stems (Cocos, Elais, Astrocaryum vulgare, Mauritia armata, Klopstockia, Chamædorea Karwinskiana) mentioned at p. 127, which are interrupted under every stoma by thin-walled parenchyma, and also with the annular layers also mentioned at p. 127, in the stems and roots of Aroideæ, and with the stegmata. Some special phenomena to be placed in this category are described by Pfitzer[1] in the case of the foliage-stem of Restiaceæ. Restio diffusus has single-layered double longitudinal rows of rod-shaped, radially elongated sclerenchymatous elements, which alternate with longitudinal bands of chlorophyll-parenchyma.

Willdenowia spec. and Leucoplocus show the same structure, with the difference that the hypodermal layers are broader, consisting of 3–4 rows. In Elegia nuda and species of Restio (R. tectorum, paniculatus, incurvatus, &c.), Thamnochortus, Willdenowia, Hypolæna, Ceratocaryum, and Leucoplocus, the very large air-cavities under the superficially situated stomata are bordered by a ring of sclerenchymatous elements, elongated and placed at right angles to the epidermis, and converging in a curve towards the inside; they are in uninterrupted lateral connection with one another, with the exception of slit-like interstices, by means of which communication between the stomatal cavity and the intercellular spaces of the neighbouring parenchyma is effected.

In the external cortex of Dicotyledonous woody plants, short sclerenchymatous elements often appear in conjunction with fibres, as annular sheaths, the formation of which, on account of their connection with the processes of secondary growth, will be dealt with in Chap. XV. Their occurrence in sappy masses of parenchyma and in the pith of Dicotyledonous plants has been already spoken of on p. 127. The small groups or nests which lie scattered in the nodes of many Potamogetons (P. crispus, densus, gramineus, perfoliatus, &c.), near the vascular bundles where they anastomose and pass out into the leaves, furnish an isolated case of the occurrence of these elements.

Sect. 128. Among sclerenchymatous masses, which strictly speaking belong to the category of hypodermal tissues under consideration, those remain to be specially mentioned to which massive hard emergencies owe their strength: e. g. tough prominent warts, as those of Aloe verrucosa, thorny teeth of leaves, as in Ilex Aquifolium, Agave, and Aloe, and spines and thorns of the different morphological categories. The epidermis itself no doubt always takes part in the sclerosis. The sclerenchymatous elements are in several cases short, e. g. warts of Aloe verrucosa, thorns of roses; usually they are elongated. The sclerenchyma, together with the sclerotic epidermis, either forms the entire mass, or it surrounds other internal tissues. E. g. the sclerenchymatous cylinder of the stem of Berberis vulgaris[2] (p. 419) sends a

[1] Pringsheim's Jahrb. VII. p. 561.

[2] Mettenius, Hymenophyllaceæ, *l. c.* p. 439.

massive branch into the thorn-leaf, which in the broad base of the thorn forms as a thick plate the larger lower half; the narrower upper half is thin-walled parenchyma, in which the vascular bundles lie. As the thorn tapers off the hypodermal sclerenchyma increases in relative extent, at the cost of the other tissue, in such a manner that in the cylindrical upper part there are only feeble vascular bundles in the middle, enclosed in scanty parenchyma, and completely surrounded by the sclerenchymatous mass, while the apex is formed of the latter and of the epidermis exclusively. The ends of the petiolar, stipular, and branch thorns of Astragalus aristatus, Halimodendron, Robinia, Maclura, Cratægus, and many thorny teeth of leaves, show a similar structure. For further details compare the works cited at p. 57, by Delbrouck, Uhlworm, Suckow, &c.; v. Mohl, Palm. Struct. p. 7; Lestiboudois, Comptes rendus, Tom. 61, pp. 1034, 1093.

Sect. 129. The sclerotic elements of the Ferns and Hydropterideæ[1] are, as explained in Sects. 26 and 28, sometimes fibrous cells containing starch, sometimes specific sclerenchymatous elements; the division of labour between the two forms is not however strictly carried out, and a sharp severance of the two is not possible. Their arrangement corresponds on the whole to the rules stated for the Phanerogams in preceding paragraphs; even the peculiarities to which attention is to be called can generally be brought under these rules as special cases.

Sclerotic *hypodermal* masses of tissue are absent in the stems or rhizomes of many Ferns, the hypodermal zone being only distinguished from the internal parenchyma, into which it gradually passes over, by the closer connection, smaller width, and somewhat thicker walls of its cells; e. g. Polypodium vulgare, pustulatum, Davallia elegans, Acrostichum vexillare, Angiopteris; Marsiliaceæ with a many-layered dense hypodermal zone of parenchyma, which passes over internally into the inner zone, which is traversed by a circle of wide air-passages. Many stems, and especially the thicker ones, have on the other hand a distinct hypodermal sclerotic zone, consisting of several or many layers of uninterruptedly united elements, which in the true Ferns always have brown membranes; in most cases this zone does not border directly on the epidermis, but is separated from it by some layers of thin-walled parenchyma. This is the case, for example, in the Cyatheaceæ, Polypodium Lingua, Platycerium, Davallia pyxidata, &c. The sclerenchymatous ring, which lies in the cortex of the thin stem of Hymenophylleæ, may just as well be mentioned here as among the instances of sclerenchyma accompanying the vascular bundles, to be brought forward later. The same applies to the dark-brown mass of sclerotic elements containing starch, which in Osmunda regalis and Todea hymenophylloides forms the principal part of the stem, and which is everywhere sharply marked off from the relatively small colourless tracts of parenchyma containing the vascular bundles. Comp. pp. 346 and 279, and Fig. 188. Sclerotic annular layers bordering directly on the epidermis occur more rarely, e. g. in the

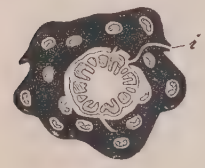

Fig. 188.—Osmunda regalis; cross-section of a vigorous stem, seen from above, i. e. from the apex of the stem, magnified about 20. *i* lowest leaf-trace bundle; a root-bundle given off from this is seen passing through the cortex.

[1] Compare the literature cited above, §§ 73–87, on the structure of the Fern-stem.

rhizome of Pteris aquilina and Polybotrya Meyeriana. The sclerosis which occurs at an early period in the cortex of the root of many Ferns was mentioned above at p. 413.

In the *petioles* and *ribs of the leaves* in Ferns, it is a general rule that a more or less strongly developed sclerotic hypodermal layer, often interrupted by the bands and islets covered with an epidermis without stomata mentioned at p. 405, lies directly beneath the epidermis, which itself not unfrequently takes part in the sclerosis. The collenchymatous zone in the petiole of the Marattiaceæ is more deeply seated, and separated from the epidermis by several layers of thin-walled parenchyma (comp. p. 120).

According to Mettenius, strands usually branch off from the hypodermal sclerenchyma in the petioles and ribs, which accompany the finer ramifications of the vascular bundles into the lamina of the leaf.

Among strictly hypodermal sclerenchymatous masses in the lamina of the leaf, the continuous layer of Acropteris australis has already been described at p. 132. Such masses occur in the form of nerve-like bands in many leaves of Marsiliæ and Ferns.

In the lamina of the aërial leaves of Marsilia coromandeliana, trichopoda, muscoides, and distorta[1], narrow colourless bands of sclerenchyma run between and in a similar direction to the nerves; some of these are small strands or even isolated fibres, adjacent to the epidermis of the lower surface of the leaf; others are thicker, extending through the entire thickness of the leaf, from one epidermal surface to the other. Hypodermal strands distributed like nerves are described by Mettenius as occurring in the segments of the lamina of the leaf of Todea Hymenophylloides, Polypodium solidum, Pteris pinnata, Davallia elata and elegans. In other Ferns the edge of the leaf or of its segments is entirely or partially rimmed by a hypodermal (many-layered) strand of sclerenchyma, which is prolonged continuously into the sclerenchyma of the petiole. This is the case in Polypodium Lingua, sporadocarpum, Brownianum, Asplenium lucidum, Polybotrya cervina, Meyeriana, Aspidium falcatum, Adiantum denticulatum, &c.[2] The strands described by Mettenius as Nervi spurii, in the leaves of many species of Trichomanes, may also be mentioned here, although, as running through a usually single-layered lamina, they do not strictly belong to this category. They consist of one or a few rows of elongated elements, which are usually accompanied by stegmata (p. 128).

Around the vascular bundles in the stem, roots, petioles, and the stouter ribs of the leaf, sclerenchyma and sclerotic cellular tissue is in many cases entirely absent, the bundle or its endodermis is surrounded by thin-walled parenchyma, which differs scarcely if at all from that lying further away from it, and is never sharply marked off. This is no doubt the case in most roots; in the stem and petiole of the Marattiæ, in the rhizomes of Aspidium Filix mas, Onoclea Struthiopteris, Polypodium vulgare, Davallia pyxidata, &c. Pteris aquilina may also be mentioned here. In several roots on the other hand, and in most stems and petioles of Ferns, distinct sclerotic sheaths and strands occur in company with the vascular bundles. This is the case, for example, in the roots of many Polypodia, as P. ireoides, vulgare, &c.,

[1] A. Braun, Monatsber. der Berlin. Acad. 1870, p. 693.
[2] Mettenius, Hymenophyllaceæ, p. 438.

Blechnum occidentale, and Scolopendrium vulgare[1], in such a form that one or more layers bordering directly on the endodermis acquire brown walls, strongly thickened chiefly on the inner side, so that these layers form either a sheath going uniformly round the whole axial bundle, or one which is interrupted, or at least thinner, over the corners of the xylem-plates.

The sclerotic sheath in stems and petioles has, in the first series of forms, the same position relative to the endodermis as in the roots. And indeed the sclerosis very often at first affects only the inner walls bordering on the endodermis, and the lateral walls of the layer of cells which is in direct contact with it; the outer walls of this layer, like those of the surrounding parenchyma, are not sclerotic, e. g. stem and petiole of Polypodium Lingua, and pustulatum, and the stem of Davallia elegans. The converse condition in the thickening of the walls occurs rarely: petiole of Blechnum brasiliense; or the sclerotic thickening of the wall exists all round, though it may be weakest on the outside: Polypodium Phyllitidis[2]. In other cases the endodermis is surrounded by an uninterrupted sclerotic sheath, consisting of one or more layers (rhizome of Polybotrya Meyeriana and Hymenophylleæ), or by an interrupted sheath, i. e. by one or several many-layered strands of sclerenchyma adjacent to it. This is the case, for example, in the rhizome of Platycerium alcicorne, and in very many petioles. In the very frequent case where the bundles in the latter have projecting corners and depressed incurvations of their surface, a definite relation between the latter and the strands of sclerenchyma exists; e. g. they lie on the concave side of the runnel-shaped bundles in the petiole of Balantium Culcita and Cyathea medullaris, in the corners of the figure × which the bundle shows as seen in cross-section, in the petiole of Scolopendrium vulgare, &c. (Comp. Russow, *l. c.* and the special pteridological descriptions.)

FIG. 189.—Cyathea Imrayana; cross-section through the living stem, natural size; seen from *above*. At *b*, *c*, *d*, foliar gaps. All the *quite black* bands and points are cross-sections of sclerenchyma; the paler ones those of vascular bundles. Within or adjacent to the foliar gaps, especially *d* and *b*, are root-bundles on their way to the periphery; *f* furrow of the base of the leaf; *a* vascular bundle of the main tube; *s* outer, *s'* inner plate of its sclerenchymatous sheath. Inside *s'* is the pith, outside *s* the cortex, with their small bundles.

In a second series of forms, the sclerenchyma accompanying the bundle is not adjacent to the endodermis, but is separated from it by a zone of delicate parenchyma, usually consisting of many layers of cells. This is the case in the stem of Todea africana, but more especially in that of the Cyatheaceæ. In most of the latter, e. g. Cyathea arborea, Imrayana (Fig. 189), Alsophila microphylla, and many others, the band-

[1] Van Tieghem, *l. c.*, p. 66, Taf. 5.
[2] Russow, *l. c.*, p. 81.

shaped main bundles of the stem are immediately surrounded by a many-layered zone of delicate parenchyma; this is completely enclosed by a stout sheath, likewise consisting of many layers, and reaching a thickness of above 1mm, which consists of acutely spindle-shaped, closely connected fibrous cells. From this sheath strands of various dimensions branch off, which accompany the medullary and cortical bundles (with the exception of the thinnest unsheathed branches), and those which pass out into the leaf; they seldom enclose these completely as they do the main-bundles; usually they are open and runnel-shaped, and placed on the inner, medullary side of the bundles, from which, however, they are separated by a broad layer of parenchyma (comp. Sect. 85). In many Cyatheaceæ, as Alsophila pruinata, blechnoides, and species of Cibotium, *all* the bundles of the stem are accompanied only by open strands or plates of sclerenchyma, which lie opposite their inner side.

Connected with these are the two thick brown plates of sclerenchyma, often fused to form a tube with only a narrow opening on one side, which run longitudinally through the rhizome of Pteris aquilina in the middle of the parenchyma, between the outer and inner tube of vascular bundles (Sect. 87). To this category belongs also the axial strand of sclerenchymatous fibres, running inside the annular vascular bundle, and often, it is true, bordering directly on the endodermis, in the rhizome of species of Pilularia and Marsilia. In the larger species of Marsilia, as M. Drummondii, and salvatrix, the outer side of the axial annular bundle is also surrounded by a tough brown sheath of sclerenchymatous fibres, which passes over internally into thinner-walled layers of cells containing abundant starch. In M. quadrifolia this sheath is replaced by a many-layered annular zone of cells bordering on the endodermis, which are rich in starch, and have brown but thin walls.

Isolated small bundles of sclerenchyma with brown membranes, or even isolated fibres, are observed here and there in the parenchyma of Ferns, e. g. the very hard small bundles in the pith of many Cyatheaceæ, where, it is true, they are often connected with those accompanying the vascular bundles as their ramifications, though they may often have an independent course, e. g. Alsophila microphylla. On the other hand, they are entirely absent in several species, e. g. in Alsophila pruinata, blechnoides, species of Dicksonia and Cibotium, according to Mettenius. Small strands, consisting of only a few fibres, ending blindly in the parenchyma above and below, or isolated fibres, traverse the parenchyma longitudinally in the rhizome of Pteris aquilina, Polypodium Lingua, Osmunda regalis, &c. In the winged edge of the base of the petiole of Osmunda and Todea similar brown fibrous tracts and fibres are arranged so as to form pinnate bands[1].

As regards the distribution of sclerotic elements in the small stem of the *Lycopodia* and *Selaginellæ*, similar general rules and also similar variations prevail, as in the case of the thinner stems of Ferns. In the stouter Lycopodia, as L. clavatum, alpinum and Chamæcyparissus (Fig. 162, p. 349), a bulky, many-layered ring of fibres surrounds the axial vascular bundle. A narrow annular zone of slightly sclerotic elements lies in the middle of the thin-walled cortical parenchyma of the foliage-stem of Psilotum. In the rhizomes of this plant and in the stems of Lycopodium Selago

[1] Compare Milde, Monograph. Generis Osmundæ; Vindob. 1868.

sclerotic layers are absent. In the stems of Selaginella the sclerosis is sometimes limited to the epidermis (S. spinulosa); in most species it further affects a hypodermal zone, which gradually passes over internally into thin-walled parenchyma; in S. rupestris the entire tissue of the stem is in the highest degree sclerotic, with the exception of the zone of lacunar parenchyma, which in this, as in all other species investigated, directly or indirectly surrounds the vascular bundles. (Comp. Fig. 131, p. 282.) The roots of the Selaginellæ and Lycopodia present essentially similar phenomena to those of the stem, with reference to the conditions in question.

CHAPTER XI.

ARRANGEMENT OF THE SECRETORY RESERVOIRS.

Sect. 130. The primary arrangement of the secretory reservoirs presents little of interest, and it has often been impossible to avoid the mention of it in preceding sections. The present Chapter, which is necessary simply for the sake of consistency, must therefore be a short one, and confine itself chiefly to references to former paragraphs.

The *sacs containing crystals* lie, in the plants enumerated in Sect. 31, to which they are peculiar, in the primary parenchyma, sometimes 'scattered' between its cells, sometimes more regularly distributed, or at definite places in definite grouping. On their distribution in the pith of Dicotyledonous woody plants, see p. 403; on their accumulation on the wall of the air-passages of Water-plants, Aroideæ, &c., comp. p. 219; on the series of raphides accompanied by mucilage in the Monocotyledons, see p. 139. It may here be mentioned more definitely than was done in Sect. 31, that the vascular bundles are occasionally, but by no means universally accompanied by series of elements containing crystals; e. g. the petiole of Cycas revoluta (p. 336); and the medullary bundles of Melastomaceæ, as Heterocentron and Centradenia spec., with longitudinal rows of sacs containing crystalline aggregations on their outer side, &c.

The *sacs containing mucilage* lie in the primary parenchyma of the plants mentioned at p. 143, and in fact principally in the foliage and cortex, usually scattered without any generally determinate order; their more regular distribution in the tubers of Orchis has already been mentioned at p. 144.

The same scattered position in the primary parenchyma of the foliage, pith, and especially of the cortex, prevails in the case of the *short sacs containing resin and gum-resin*, of the families mentioned at p. 145.

The *long* sacs of this category, and the tannin-sacs, have already been discussed at p. 146, &c. Comp. further Sect. 48, especially p. 199, and Chap. XII.

CHAPTER XII.

COURSE OF THE LATICIFEROUS TUBES.

Sect. 131. The laticiferous tubes[1], in most plants which are characterised by their occurrence, traverse the entire body of the plant as a continuous system. Exceptions to this rule seem, however, to occur; in the roots of Asclepias curassavica, and Cornuti, and of Periploca, I could not find them, but will not assert their absence with complete certainty; in the roots of Ficus elastica I only find them in the secondary bast.

As regards their relation to the other tissues, we may call them, as already indicated above, companions, or in some places even representatives, of the sieve-tubes. The latter relation is especially manifest in the secondary bast of many plants, to which we shall have to return, below, Sect. 163. In the primary groups of tissue the laticiferous tubes are distributed—

(*a*) In the roots within the phloem of the vascular bundle. Only in the case of the Euphorbiæ investigated do others occur in addition, which arise as branches from those of the cotyledonary node, and lie close under the epidermis, separated from the latter only by a few layers of cells (comp. p. 196)[2].

(*b*) In stems, petioles, and ribs of the leaves, the main courses or main trunks of the tubes lie chiefly in the tissue surrounding the phloem-portions of the vascular bundles, following the longitudinal course of the latter, and, as seen in cross-section, scattered without strict regularity among the surrounding parenchyma. If the phloem is sheathed by a strand of sclerenchyma they lie outside the latter. In addition to these tubes, other smaller ones occur in certain cases, e. g. Cichoriaceæ and Papaver, which run in the phloem itself. In milky plants provided with phloem-portions towards the pith, or with separate medullary bundles of sieve-tubes, these also are accompanied by laticiferous tubes (comp. p. 338).

In the foliar expansions, the tubes on the one hand still follow the higher orders of ramification of the bundles; on the other hand, in the majority of cases, they send out branches which leave the paths of the vascular bundles, force their way in all directions between the cells of the parenchyma, and end blindly, sometimes in the interior of the latter, sometimes at the inner surface of the epidermis. In the case of Siphocampylus manettiæflorus, Trécul even states that the ends of the branches pass between the cells of the epidermis, as far as its outer surface. In many milky Dicotyledons, branches of the tubes also traverse the cortex of the stem, partly in the internal parenchyma, partly hypodermally. In the succulent Euphorbiæ possessing

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[1] See Chapter VI, and the literature there cited.

[2] [Compare Scott, *l. c.*, p. 143. (See p. 193).]

rudimentary or very fugacious leaves, and in the Asclepiadeæ, they branch off at all points from the main trunks, and are distributed through the massive cortical parenchyma in all directions as far as the epidermis, having an oblique and crooked course. In non-succulent stems with well-developed, persistent foliage leaves, longitudinal tubes occurring in the hypodermal cortical layer, and branched off from the main trunks in the nodes, are, judging from Trécul's statements and the phenomena in Euphorbiæ to be communicated below, at any rate much more frequent than has been represented by most previous observers.

In many cases also, branches, which are usually thick tubes, pass from the main trunks into the pith; in the case of medullary bundles of sieve-tubes, they branch off from the main-stems which accompany the latter (Hoya, Asclepias spec.) In plants without medullary sieve-tubes, as Ficus and Euphorbiæ, they arise as branches from the main trunks, principally, but as shown by the succulent Euphorbiæ not exclusively, in the nodes. According to the particular case, they are either inserted in the parenchyma throughout the entire thickness of the pith, e.g. Ficus, or they are confined to its periphery, e.g. Euphorbiæ.

According to the particular families, and even the species, the general rules stated above are subject to manifold variations. The most important details will be given below, reference being made to Chap. VI, and the special works there cited. Some data referring to the secondary wood and secondary bast, belonging to Chaps. XIV and XV, may here be anticipated.

I. ARTICULATED LATICIFEROUS TUBES.

1. **Cichoriaceæ.** In the stem of those species investigated, which have ordinary collateral bundles within the boundary of the plerome, the tubes in the first instance lie around the phloem of each of these bundles. Their longitudinal main trunks here form, as seen in cross section, a single curved row, often interrupted by parenchymatous cells, at the boundary towards the cortical parenchyma; their numerous transverse anastomoses pass along the outer surface of the approximately semi-cylindrical phloem, which is usually destitute of any sclerenchymatous support. These peripheral tubes are the largest. In the stems of Chondrilla, Taraxacum, Apargia, and Cichorium, no other laticiferous tubes are present. The bundles in the lower part of the stem of Sonchus tenerrimus, Picridium tingitanum, and, in a slight degree, of Lactuca virosa, have sieve-tubes on the inner side of the xylem also, and are then accompanied here also by laticiferous tubes, which are connected with those outside by branches passing right round the vascular bundle (Trécul). Finally, where, as in the investigated species of Lactuca, Sonchus, Scorzonera, Tragopogon, and Hieracium, small medullary bundles of sieve-tubes are present, the latter each contain some laticiferous tubes, which run parallel to the sieve-tubes, and anastomose with one another between them, without however having an open communication with the sieve-tubes. According to Trécul, anastomoses take place along the entire internode between the nets of tubes accompanying the different vascular bundles. In all plants of the family in question, they are especially numerous in the nodes, both between the peripheral tubes accompanying the vascular bundles, and between these and the medullary tubes, the latter occurring together with the anastomoses described at p. 231, between the groups of sieve-tubes belonging to the two regions. In the nodes the nets of laticiferous tubes of the stem are further continued into those of the petioles and of the axillary branches.

In the petioles and ribs of the leaves, the nets of tubes accompany the vascular bundles with the same arrangement as in the stem, and finally their branches, which end

blindly, either terminate together with the last vessels in the parenchyma of the leaf, or similar terminal branches are sent out as far as the epidermis.

For the course of the tubes in the peduncle and receptacle, essentially the same rules hold good as for the stem: some branches of them accompany the small vascular bundles which traverse the pistil, corolla, and stamens (Hanstein).

In the roots the tubes lie in the phloem-groups of the original vascular bundles, and thus within the pericambial zone—at least in Tragopogon and Scorzonera hispanica.

They never enter the xylem groups unless it be in the ultimate ramifications of the bundles, where they are in close contact with the tracheides, and in the nodal anastomoses, which pass through the medullary rays, between the medullary and the peripheral bundles, where they may come to lie close to the vessels.

2. The nets of laticiferous tubes of the **Campanulaceæ** and **Lobeliaceæ** are in general quite similar in form to those of the Cichoriaceæ. In their distribution a difference is in so far observable, that the chief seat of their occurrence is the internal phloem-region, which lies towards the xylem-portions of the bundles. In the periphery of the phloem and the parenchyma of the external cortex they are in many cases entirely absent, or very isolated (Lobelia inflata, syphilitica, urens, Adenophora Lamarckii, Phyteuma Halleri, spicata, Campanula sibirica, medium, ranunculoides, grandis, lamiifolia); more rarely they are abundant (Tupa salicifolia, Isotoma, Centropogon, Piddingtonia spec.), and especially in Tupa Feuillei, Ghiesebrechtii, and Musschia aurea, where they penetrate up to the epidermis. In the case of Siphocampylus manettiæflorus, Trécul states that individual ends of branches penetrate as far as the surface of the epidermis, and even project there as small papillæ.

In those Campanulaceæ which have sieve-tubes on the inner side of the woody ring, or in the medullary bundles, the phenomena above mentioned are complicated by the occurrence of laticiferous tubes accompanying the latter, as in the case of the Cichoriaceæ with similar structure. They are absent in the xylem, in the secondary ring of wood, and in the parenchyma of the pith in all Campanulaceæ investigated, and in many Lobeliaceæ. In other plants of the latter family on the other hand, e. g. Centropogon surinamensis, Tupa salicifolia, Ghiesebrechtii, Feuillei, Siphocampylus manettiæflorus, microstoma, and Lobelia laxiflora, Trécul found them scattered at the periphery, and more or less deep in the interior of the pith, and found that these medullary tubes are in communication with the cortical ones by means of branches traversing the woody ring.

3. The laticiferous tubes of the **Papayaceæ**, investigated in Papaya vulgaris, Vasconcellea monoica, cauliflora, and microcarpa, form in the stem of these plants an abundantly ramified and anastomosing net-work of tubes, extending both through the highly parenchymatous primary and secondary wood, and also through the medullary rays and the bast-region. The main trunks have an approximately vertical course and form interrupted rows approximately concentric with the circumference of the stem; the separate portions of these rows everywhere alternate variously in wood and bast, with parenchyma, vessels, and sieve-tubes. The neighbouring tubes are connected laterally with each other by means of exceedingly numerous wide anastomoses. Similar anastomoses occur in the most various particular forms, between the different groups and rows, both in radial and tangential direction, the radial connections being often effected by long transverse branches with an approximately horizontal course. Blindly ending branches and branchlets further occur with varying frequency. The tubes are usually separated from the vessels by at least one layer of parenchyma, some however are in contact with them, and as discussed above (Chap. VI) there is perhaps open communication between the two. Into the pith of the internodes, which soon disappears, the tubes do not enter; they form, however, a complex network, anastomosing on all sides in the medullary disk, which is persistent in the nodes. In the primary cortical parenchyma, Dippel alone found isolated tubes, accompanied as a rule by parenchymatous cells containing crystals near the outside of the bundle of bast-fibres, and connected with the internal tubes by very elongated horizontal transverse branches.

In the leaf-stalks and ribs of the lamina they follow the vascular bundles, often accompanying and touching sieve-tubes and vessels. In the parenchyma of the leaf they end with numerous anastomosing branches.

After the commencement of secondary thickening the root has a similar structure, and a similar distribution of the laticiferous tubes to that in the stem.

4. Among the milky **Papaveraceæ** two types of laticiferous tubes are to be distinguished. The one is represented by the investigated species of Papaver, Rœmeria, and Argemone, and shows tubes which arise from elongated elements, but only rarely allow traces of the original cross-walls to be recognised in the mature condition; these are connected into a net by more or less numerous anastomoses. In the stem and petioles they lie in tangential curved rows in the phloem of the vascular bundles, in each one of which they anastomose in the transverse direction, though there are no anastomoses between those of the different bundles of an internode. In the (secondarily thickened) root, in the cortical parenchyma, and especially the bast layer, and also in the parenchyma of leaves, pericarps, &c., they end in an abundantly ramified net.

The other type is represented by Chelidonium, and is characterised by the facts that the cross-walls of the elements merely have one or more large perforations in the middle, while on the other hand their edge remains preserved, and that reticulate connections do not occur. On account of the partial persistence of the cross-walls, the tubes appear at the first glance like rows of cells, the articulation of which comes out all the more sharply, as they are usually somewhat constricted at the cross-walls (cf. Figs. 80, 81, p. 189). Sometimes when two tubes are in direct lateral contact, perforations appear to occur in the lateral wall also. In the older roots the tubes are often branched, owing to the fact that a series of elements is continued from one point into two diverging series, which meet at an acute angle; and the individual elements are short, on the average 2–4 times as long as broad, being of about the same length as the neighbouring parenchymatous cells, and elements of the sieve-tubes. In the parts of the plant above ground, on the other hand, the elements are very elongated, so that their ends more rarely come into view in preparations. In the (older) roots, the tubes in the bast-layer are so distributed in groups, forming concentric, irregularly interrupted rows, that every group usually lies in the neighbourhood of a small group of sieve-tubes, surrounded by masses of parenchyma containing starch. In the stems and petioles narrow laticiferous tubes lie scattered in the vascular bundles within the phloem, and at the periphery of the xylem; they further occur externally to the vascular bundles, on the outside of the fibrous bundles bordering on the phloem, and also isolated in the peripheral (cortical) parenchyma. In the lamina of the leaf and the parts of the flower the system of tubes ends in the reticulate form described above for other cases.

In other Papaveraceæ, especially Macleya cordata and species of Glaucium (I investigated Gl. luteum), no doubt also in Eschscholtzia (which, however, requires further investigation with reference to the statement of the anonymous writer in the Botanische Zeitung, 1846), and in the Fumariaceæ, no laticiferous vessels whatever are known. A red sap, which is on the whole clear, and mixes both with water and alcohol without turbidity, appears conspicuously on cut surfaces of the rhizome of Sanguinaria: it is contained in large, thin-walled, roundish or shortly cylindrical cells or sacs, which are abundantly distributed through the whole parenchyma, sometimes isolated between (starch-containing) parenchymatous elements, sometimes, and especially in the cortex, forming continuous longitudinal rows (cf. Hanstein, *l.c.*, Taf. I). In the stem and petiole, which I have not investigated, these sacs are elongated cylindrical or prismatic. Neither their walls nor their contents show the properties characteristic of laticiferous tubes; they were therefore mentioned above at p. 147.

The same holds good for the sacs filled with a clear reddish-yellow sap, which are scattered through the parenchyma in the root of Glaucium luteum, and which, according to the form of the contiguous elements, are more or less longitudinally extended. In the stem and foliage of species of Glaucium (cf. Trécul, *l.c.*) they are absent. In the

rhizome and stem of Macleya cordata, similar sacs, sometimes very much elongated, are scattered in large numbers about the periphery of the ring of vascular bundles, and in the medullary rays. As the parts grow old the reddish-yellow colour of the sap disappears. The elongated sacs bordering on the fibrous bundles of the bast then acquire thickened walls, like sclerenchymatous fibres.

5. According to their structure, the latex- and tannin-tubes of many **Aroideæ**[1] belong to this part of our subject. Their main trunks lie in the periphery of the phloem of the vascular bundles, usually two or more together, in collateral bundles situated as a rule symmetrically on each side, in the 'compound' bundles less regularly distributed. In their most perfectly developed form, in Caladium and its allies, Alocasia, Xanthosoma, Syngonium, &c., they constitute thin-walled sacs, about equal to the sieve-tubes in width, following the longitudinal course of the bundles; at the limiting surfaces of the surrounding parenchymatous cells they send out numerous, pointed or blunt, blind protrusions, which penetrate between the latter. Other protrusions are extended to form longer tubular branches, penetrating between the surrounding tissue-elements, and these also sometimes end blindly, often showing somewhat enlarged ends, while sometimes they meet similar branches of neighbouring trunks, and enter into open communication with them. The network of tubes thus formed is extended throughout the parenchyma, not only between the vascular bundles, but also not uncommonly in the parenchymatous cortex, as far as the under side of the epidermis.

The branches of the network of tubes also run towards the tracheæ, attach their ends to the latter, and, as stated above, frequently enter into direct communication with them.

The contents of these tubes consist of a finely granular fluid, which, according to Trécul, is milky in species of Syngonium and Xanthosoma, in other cases only a little turbid, and very rich in tannin, so that after the action of iron salts or potassium bichromate the net-work of tubes comes out darkly stained.

Other Aroideæ (Richardia africana, Arum vulgare, Dracunculus, Aglaonema simplex, Dieffenbachia Seguine, and species of Philodendron) have no laticiferous tubes, but contain longitudinal rows of elongated cylindrical or prismatic sacs in the periphery of the phloem, with the same arrangement as the trunks of the net-work of tubes described above. They contain the same turbid contents as the tubes described (in Dieffenbachia Seguine according to Trécul they are without tannin), but they are separated by cross-walls and are without lateral anastomoses, only sending out short blind protrusions between the limiting surfaces of the neighbouring parenchymatous cells.

A third category—Heteropsis, Lasia, Scindapsus, Monstera, Anthurium, Acorus, &c.—is wholly destitute both of the tubes described, and of sacs.

That these net-works of tubes arise from the union of originally separate, branched cells, is shown both by the history of their development, and by comparison with the sac-tubes of the second category.

6. In the species of the genus **Musa**, the vascular bundles in the stem, the petiole, the midrib, and the lamina of the leaf (especially also in the fruits) are accompanied by wide laticiferous tubes which are arranged symmetrically, 2–6 around each bundle, and in fact around both phloem and xylem; usually, however, they are not in direct contact with the bundle, but are separated from it by 1–2 layers of parenchymatous cells. The tubes in the stem and petiole are unbranched, and each consists of a row of cylindrical sacs standing vertically one above another, which are about four times as long as broad, and are united to form a continuous tube by means of a wide round opening in every cross-wall. Round every cross-wall the tube is somewhat constricted, as was well represented even by P. Moldenhawer. The tubes contain large, homogeneous, strongly refractive spheres

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[1] Karsten, Monatsber. d. Berliner Acad. 1857; Gesammelte Beiträge, p. 253.—Trécul, Van Tieghem, Hanstein, *l. c.*

(of resin?), suspended in a fluid, which is almost always in the highest degree rich in tannin; in M. zebrina alone it is frequently destitute of tannin, according to Trécul. After the action of alcohol or potassium bichromate, a very sharply defined coating of the wall appears, resembling a contracted primordial utricle, and this likewise shows the tannin reaction (investigated in M. Cavendishii).

Besides that in the laticiferous tubes, tannin also occurs as a principal constituent of the contents in single scattered, short, parenchymatous cells, and in isolated cambiform cells in stem and petiole.

The other Musaceæ investigated have no laticiferous tubes, in spite of the fact that in the rest of their structure they agree entirely with Musa. In place of them spaces usually filled with tannin are found in cross-sections of Urania speciosa and Strelitzia, in the neighbourhood of the thicker vascular bundles; these appear to be the laticiferous tubes; the longitudinal section, however, shows that they are only parenchymatous cells or sacs with the contents indicated, which do not even form uninterrupted longitudinal rows one with another. Those which succeed one another at different heights rather belong, sometimes to one and the same, sometimes to various other rows of parenchyma. In the rest of the parenchyma, and in the phloem portions of the vascular bundles, scattered tannin-sacs occur, as in the equivalent parts of Musa. Heliconia speciosa and H. Bihai, according to Trécul, never show cells or sacs filled with tannin, with the exception of single scattered ones in the phloem of the vascular bundles. The same applies to H. pulverulenta Lindl. Finally in Ravenala madagascariensis, &c., Trécul could not find tannin at all, only the wall of individual cells of the leaf-sheath showed an indication of blue colouring after the action of iron sulphate for twenty days.

II. NON-ARTICULATED LATICIFEROUS TUBES.

7. **Euphorbiaceæ.** Of this family a number of species of Euphorbia have been investigated with accuracy. In the shrubby, more or less succulent forms of hot countries, as E. splendens, E. Caput Medusæ, canariensis, rhipsaloides, &c., the stem shows a relatively thin ring of vascular bundles, or of wood and bast, which encloses a bulky succulent pith, and is surrounded by a layer of cortical parenchyma, which is also thick. The stouter, thick-walled, main trunks of the laticiferous tubes run close to the outside of the ring of bundles; they are scattered in the cortical parenchyma, either singly or in small groups. Their course is in general longitudinal, though not rectilinear, but undulating both in the radial and tangential direction. They give off numerous branches which are further ramified through several degrees (cf. Fig. 84, p. 191). Those of the first degree do not differ from the main trunks, their direction also is the same. The branches of higher degrees become successively narrower and thinner-walled, those of the last degree have blunt blind ends. The direction of the higher degrees of ramification is very various; sometimes their course, like that of the primary tubes, is longitudinal; sometimes they penetrate in a curved and undulating course between the cells of the cortical parenchyma, sometimes individual branches pass through the latter towards the surface, and reach the inner side of the epidermis, where they end blindly, either at once, or after running for some distance below it. Other less numerous branches pass through the medullary rays into the pith, in the peripheral region of which they divide into numerous thick branches, each of which usually has an isolated longitudinal course. We therefore find laticiferous tubes scattered in the parenchyma, on the medullary side of the wood also. Reticulate anastomoses do not occur. Where an H-shaped connection between two tubes is found, this depends merely upon the form and direction of blindly ending branches. In those species which have developed leaves (E. splendens) the laticiferous tubes enter them, at first following the vascular bundles, and then sending out numerous branches from these, through the parenchyma, which run in the most various directions, and at last end blindly.

The tubes are uninterruptedly continuous throughout the entire plant. No trace of an articulation ever occurs (with exception of the formation of isolated cross-walls, mentioned at p. 196). It has never been found possible to dissect out from a piece of a stem, a tube of which even one of the main branches or trunks was closed blindly at both ends. Trécul isolated a portion of a tube from the stem of E. globosa, the united ramifications of which were together 93·5 mm in length, and had 120 points of branching; yet 7 main branches and many smaller ones were torn off. I have isolated many main branches from the stem of E. splendens up to 50–70 mm in length, without ever finding a blind end to them (i. e. apart from the shorter lateral branches). In the growing-point of the stem, branches, and roots, and in young rudimentary leaves, the laticiferous tubes extend close up to the extreme apex, even before the development of the first elements of the vascular bundle, and are always to be clearly recognised as branches which start from the tubes in older parts, and penetrate into the meristem in course of formation. Even in the seedling (investigated in the case of embryos of E. resinifera Berg.) the laticiferous tubes behave as described above, with the sole difference that their ramifications are as yet less abundant than in the older plant. It follows from these facts, that all the tubes of the plants in question are branches of a few primary ones, which, originating in the embryo, grow on and on with the stock, and put out their branches into the newly formed meristems and tissues. Cf. Chap. VI.

The embryo and seedling of the native, herbaceous Euphorbiæ (Tithymalus, Klotzsch and Garcke) show the same points of origin of the tubes as the species discussed above, while the mature plant shows the same continuity of all of them as branches of a few primary trunks, which first appear in the cotyledonary node (cf. p. 196). In correspondence with the entire growth and structure, the course of all their branches is different from that in the succulent shrubby forms, especially in the stem. In the internodes of E. Lathyris (cf. Fig. 190) the thicker main branches of the tubes lie in the parenchyma of the cortex, outside the fibrous strands which support the phloem of the vascular bundles, occurring isolated and in small numbers between the parenchymatous cells. They here have a fairly straight course through the internode, and are little, if at all, branched. In the node, on the other hand, abundant ramifications, with a variously curved and intertwined course, occur (Fig. 190), sending out from here further branches, some of which ascend, with the arrangement described, into the cortex of the next higher internodes, some enter the leaves and axillary buds, at first following the vascular bundles, while others finally, in these regions, pass between the vascular bundles into the pith of the stem, and then descend scattered singly between the parenchymatous cells of the permanently succulent peripheral portion. The inner part of the pith, which soon dries up, contains no laticiferous tubes. Finally, numerous thin branches proceed from the node; these pass along the internodes near the epidermis, and together form a hypodermal system of tubes. They ascend vertically from the node into the internode next above, and usually run between the first and second hypodermal layer of parenchyma, more rarely directly below the epidermis, with a straight upward course and ramifying here and

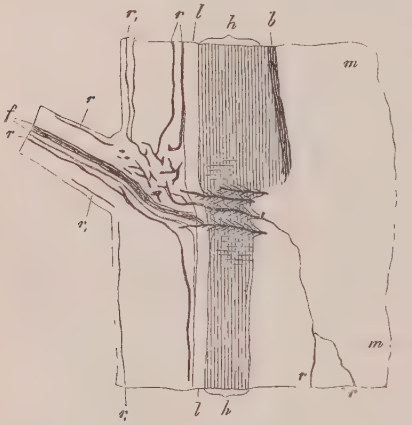

FIG. 190.—Euphorbia Lathyris; radial longitudinal section through half the node and the neighbouring portions of the internodes of a mature stem, together with the base of a leaf; slightly magnified; *m* pith, *b* portion of a bundle of the leaf-trace, *h* secondary wood, *l* bast layer of the stem. The dark lines marked *r* are the laticiferous tubes; the short black lines and points in the node are fragments of the web of laticiferous tubes occurring there. From this two laticiferous tubes belonging to the bast, and two hypodermal ones are seen passing upwards, while four pass towards the pith; *r* hypodermal laticiferous tubes.

there at an acute angle. At the next point of insertion of a leaf, which they reach on their way, many of these branches, preserving the same position relatively to the surface, bend out into the petiole, pass through this to the lamina, and here divaricate near the epidermis of the lower surface. The great majority of the branches, which are distributed and terminate in this region, certainly belong to the hypodermal system in question. The latter stands in no other connection with the main trunks belonging to the bundles, than that which depends on its points of origin in the nodes; it is separated from them in the internodes by many layers of lacunar cortical parenchyma. Its presence may always be recognised, even on the most superficial observation, by the fact that from almost every slight prick into an internode, though far from penetrating the cortical parenchyma, drops of latex exude. The great majority, at any rate, of the Tithymalus-Euphorbiæ have essentially the same arrangement of the laticiferous tubes; e.g. E. Cyparissias, sylvatica, Characias, Peplus, Lagascæ, also E. Myrsinites, which is characterised by especially large and numerous tubes; many differences occur, it is true, according to the particular species, which chiefly affect the greater or less frequency of hypodermal tubes, the presence or absence of medullary ones, &c., and may here be passed over.

No accurate investigations of the laticiferous tubes of other Euphorbiaceæ exist. Hanstein says: 'Where the development of the latex itself is inconsiderable, as in Ricinus, Mercurialis, and other genera, there we find its vessels also less abundantly distributed, and less conspicuous. They possess but scanty ramifications and anastomoses, but on the other hand they have more strongly thickened walls.' Vogl mentions the laticiferous tubes in the outer and inner cortex of Hippomane Mancinella, and calls attention to the great similarity of those of Hura crepitans with those of the succulent Euphorbiæ.

8. The laticiferous tubes of the **Urticaceæ**, **Apocyneæ**, and **Asclepiadeæ**, agree, so far as investigations extend, with those of the Euphorbiæ in all essential points, as regards both their form, structure, and ramification, and their development and distribution. This agreement becomes especially conspicuous if the succulent leafless Asclepiadeæ, of the genera Ceropegia and Stapelia, be compared with the Euphorbiæ of similar habit. On the average the laticiferous tubes of the families in question are narrower and thinner-walled than those of the Euphorbiæ, but very thick ones occur, e.g. in species of Nerium and Ficus. With respect to the abundance in which they occur in the cortex and pith of the stem, the divarication of their branches in the parenchyma of the leaf, &c., the same differences between individual species of each family prevail, as within the genus Euphorbia. While, e.g. in thick-leaved species of Ficus, they extend their branches abundantly through the parenchyma of the leaf, up to the epidermis, in the leaf of Humulus, according to Hanstein, they are confined to the vascular bundles, and do not extend into their ultimate ramifications. Especially abundant subepidermal ramifications are described by Trécul in the leaves of the Asclepiadeæ, Echites peltata, and Arauja sericophora.

Among Asclepiadeæ and Apocyneæ, a larger number of forms have been investigated, especially by Trécul, e.g. Hoya carnosa, species of Asclepias (A. Cornuti, curassavica, &c.), Physostemma, Centrostemma, Cryptostegia, Stapelia, Ceropegia, Echites, Arauja, Nerium, Vinca, Apocynum, Plumiera, Tabernæmontana, and many others.

Among the Urticaceæ, more accurate investigation has been chiefly confined to species of Ficus (F. carica, elastica, repens). Minute comparative investigations on the course and development of the tubes are however still to be desired, not only for the orders last mentioned, but also for the Asclepiadeæ and Apocyneæ (cf. p. 198).

CHAPTER XIII.

PRIMARY ARRANGEMENT OF INTERCELLULAR SPACES [1].

Sect. 132. The *air-containing*, and sometimes water-containing intercellular spaces have been described in Sect. 51, and in the paragraphs treating of the stomata, the parenchyma, and the structure of the vascular bundle, and their arrangement was described at the same time. Here it is only necessary again to bring forward the fact already mentioned on p. 210, that all the air-spaces in question together form a connected system of communicating tubes throughout the whole plant. Where there are stomata this system opens first into the 'respiratory cavities' below them, and then through the slits themselves it communicates with the outside, and thus in the terrestrial and swimming plants, which we have more especially under consideration, it also communicates directly with the surrounding atmospheric air [2].

Sect. 133. Of the *intercellular secretory reservoirs* the short *cavities* have also already been dealt with as regards their distribution, on p. 207.

It therefore remains still to treat of the arrangement and course of the secretory *passages* and *canals*, and at the same time to take into consideration many phenomena of their structure, which were passed over before (comp. p. 206), with constant reference of course to Sect. 50.

The secretory passages traverse the members of the plant longitudinally at first as prismatic tubes, which usually acquire a round or elliptical transverse section: rarely they appear as more or less elongated sacs with both ends closed blindly, as in the exceptional cases of Tagetes and Mammea, quoted on p. 201, and in many Coniferæ. In the great majority of cases they are in open communication throughout the plant, forming a system of tubes, which branches and anastomoses—especially, but not exclusively, at the nodes—and may send out blind, or also anastomosing branches into the foliar expansions.

Their arrangement in the members varies greatly according to the groups and even the species, nevertheless it is regular and constant within each of these circles of relationship. Besides those which appear constantly in one species or group of different rank, there are in many cases accessory passages, which may occur in varying number according to the individual or species, or may even be absent, e. g. leaves of Pinus, medullary passages of the Terebinthaceæ, Coniferæ, &c.

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[1] [Compare v. Höhnel, Verhältniss der Intercellularräume zu den Gefässen, Bot. Ztg. 1879, p. 541; also, Ueber Harz-räume im Kork-gewebe, Bot. Ztg. 1882, p. 161, and über gefässführende Hölzer mit Harzgängen. Ibid.]

[2] Compare Sachs, Experimentalphysiologie, p. 254.

Any other form of tissue, and any region may contain secretory passages, even the primary xylem of the bundles. Still in this relation also the phenomena are constant, according to species and groups, while in individual cases all possible combinations occur, as is obvious from the following synopsis of the most important known examples, and from the works therein cited, which are to be compared for further details. For the sake of clearness, and in order to avoid repetitions, the secondary changes belonging to the subjects of Chaps. XIV and XV will often be mentioned in the following pages.

The mucilage-canals of the *Marattiaceæ*[1] traverse the parenchyma of the pith and cortex of the stem in great numbers, and branch and anastomose frequently. They are continuous from the cortex into the roots, in which they pursue a directly longitudinal course towards the apex, and here end in the meristem; and into the foliar organs, having a similar straight course in the petiole and rachis, with few branches and anastomoses. Their endings in the foliar organs have not been exactly investigated; thorough descriptions of their course in the segments of the lamina are also wanting.

The leaf of *Lycopodium* inundatum (also of L. alopecuroides)[2] is traversed on the posterior side by a mucilage-canal, which runs from apex to base: here it enters the cortex of the stem for a short distance, and there ends blindly. The mature canal is limited, as in Marattia, by closely-connected cells of the adjoining parenchyma, but irregular club-shaped cells are seated upon the latter, which project like hairs into the cavity of the canal. In the young leaf these cells form a strand 4–5 rows thick, where the future canal will be, and they have the form of angular meristematic cells; as the leaf unfolds they separate from one another, while the surrounding tissue extends to a corresponding extent, and they elongate to a club-shape, while the mucilage appears between them. They thus constitute the epithelium of the passage, which is still more dissociated than that in Marattia. A similar small passage is found in the marginal expansions on the dorsally winged ridges of the leaves of the spike in L. annotinum.

In the stem of the *Cycadeæ* mucilage-passages are also distributed through the parenchyma, in specially large numbers in the cortex: they have branchings and anastomoses. But branches from those of the stem always pass into the leaves, and there end. They traverse the petiole and rachis of the pinnate leaves longitudinally, in varying number according to species and individual—in one small leaf of a seedling of Zamia longifolia I found, e. g. in the petiole only two, in the larger leaves of stronger plants they are numerous, and their distribution in the parenchyma is generally irregular. They enter the pinnæ only in forms of Dion, Encephalartos, and Stangeria[3], in the first genus running sometimes above the vascular bundles, in Encephalartos between them, and indeed alternating regularly with the parallel vascular bundles in the same plane with them and at equal distances; in the pinna of Stangeria they lie above and below the vascular bundles of the rib, without passing out laterally into the lamina. In the specimen examined one central bundle, and one lateral one near it on either side ran into the rib. One mucilage-passage lies between the middle bundle and the upper epidermis, and one on each side between the lower epidermis and the gap which separates the middle one from the lateral bundles.

Among the *Coniferæ* all investigated species, with the single exception of Taxus, have resin-passages or resin-reservoirs, which vary in distribution and number according to the species.

Starting from the leaves[4], in those examples which have one median vascular bundle or pair of bundles—as in the investigated species of the Cupressineæ, Sequoieæ,

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[1] Harting et de Vriese, Monogr. des Maratt.—Frank, *l. c.*

[2] Hegelmaier, Botan. Zeitg. 1872, p. 844.

[3] Kraus, Cycadeenfiedern, *l. c.* p. 328.

[4] Thomas, Coniferenblätter, *l. c.*

Taxineæ, the genera Saxegothea, Dacrydium, Podocarpus (excepting the section Nageia), and Tsuga with exception of T. Douglasii Carr.—there is *one* constant resin-passage between the bundle and the epidermis of the lower surface of the leaf, either close to the latter, often as a keel or ridge projecting outwards as in species of Juniperus, Thuja, and Biota, or deeply embedded near to the bundle, as in Cunninghamia (Fig. 191). Besides these there are in many species (e. g. Cryptomeria) accessory passages corresponding in their arrangement to those which are constant in the Abietineæ. One of these lies (with the exception as above of Tsuga) at each lateral margin of the leaf close to the upper surface; either this alone is present, e. g. always in Larix and Cedrus, or three are also accessory ones in the hypoderma, the number and arrangement of which vary

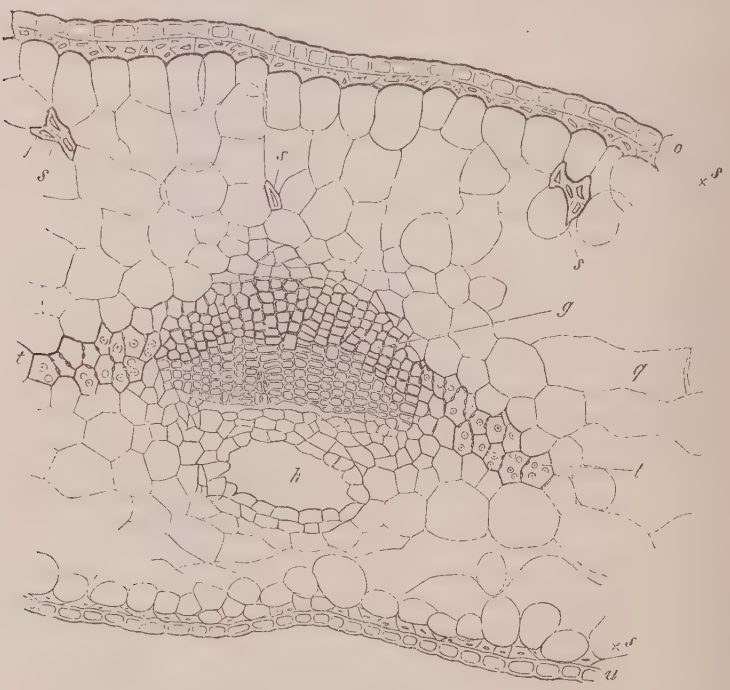

FIG. 191.—Cunninghamia sinensis; transverse section through the leaf (220). *u* lower, *o* upper surface; *h* resin passage, ×*s* hypodermal fibres, *s* sclerenchymatous fibres scattered in the parenchyma, *g* xylem of the median bundle, *l* its border of tracheides. Below, and towards the resin passage, is the thin-walled phloem; the white band at its margin towards the parenchyma surrounding the resin passage is the compressed primordial tissue of the phloem. *q* transversely-elongated parenchymatous cells of the middle of the leaf.

according to both species and individual: e. g. in the needles of Pinus sylvestris to such an extent that 1–22 of them have been observed.

In the leaves of Sciadopitys 4–10 passages lie under the epidermis, which are distributed in varying symmetry over the margin and lower sides in relation to the simple or double leaves.

The leaves of Araucaria, Dammara, and Ginkgo, with several vascular bundles, are traversed by at least as many passages as bundles; they alternate with the latter in almost the same plane.

The passages in most cases pass continuously through the elongated leaves from the base upwards, and end blindly at a distance from the apex, which varies sometimes with the individual, sometimes with the species. Thus the median passage in species of Podocarpus, stops far below the middle of the leaf. In the lamina of Ginkgo, in place of the

uninterrupted canals, there are between the vascular bundles short cylindrical sacs 1mm or more in length, which are closed blindly at both ends. In the scale-like leaves of many Cupressineæ, as Thuja, &c., the passages are of course short, and relatively broad, and may more properly be termed gaps or cavities.

The passages and cavities of the leaves are continuous from the insertion of the latter into the primary cortex, and there pass perpendicularly downwards. In the transverse section they form a ring lying in the cortical parenchyma, and are generally grouped according to the arrangement of the leaves. At any rate in a large number of forms they end blindly above the insertion of the lower leaves, without open communication with other passages. Thus in the investigated Cupressineæ with whorled leaves, as Thuja, Biota, Juniperus. In J. communis e. g. a large passage enters the stem from each leaf, and there runs downwards, in one of the three angles, to a point close above the plane of insertion of the next lower whorl, and there ends.

On the other hand, in Pinus sylvestris, Abies excelsa, and, according to Mohl's statements [1], in the Abietineæ generally, the passages which come from the leaf, after descending through numerous internodes, open into others belonging to lower leaves; the point of confluence corresponds to a widening of the passage on which the higher one is inserted. The passages of the primary cortex are therefore connected into a system of communicating canals. The composition of this, as well as its distribution in individual forms, remains to be more exactly investigated.

The great majority of the Coniferæ have no others in the primary tissues of the stem besides the cortical passages above mentioned. This is the case in all investigated Taxineæ except Ginkgo; most Cupressineæ, Podocarpus, Cedrus, Abies, Tsuga, Pseudolarix.—Araucaria Cookii and Brasiliensis, and Widdringtonia cupressoides, have besides, according to van Tieghem, a passage in the phloem of the primary vascular bundles, which stops short before the exit of the bundle into the leaf.

In the species of Pinus s. str., Larix, Picea, Pseudotsuga there is also a passage which is not continued into the leaf, but it does not lie in the phloem; but in the xylem of the primary bundles.

Finally, Ginkgo biloba has large passages in the pith in addition to the cortical ones. In transverse section there are one or two present, and so arranged that they correspond to the insertions of the next higher leaves. Nevertheless they end blindly both downwards and towards the petiole, though the canal situated in the latter above the vascular bundles lies in the ideal prolongation of the medullary canal situated opposite the leaf in question.

In the *Root* the passages of the primary cortex are wanting in all investigated Coniferæ, and in most cases also those of the vascular bundles. In the latter, however, they are found in certain species or groups; thus, according to van Tieghem, in Araucaria Cookii and Brasiliensis there are five in each phloem portion of the diarch bundle, in Widdringtonia cupressoides one in the same position. The Cedars and Firs (Cedrus Deodara, Abies pectinata, balsaminea, Brunoniana) and Pseudolarix Kämpferi have a canal in the middle of the radical bundle. In the Pines (Pinus s. str.) and Larix one passage lies between the two shanks of each vascular plate, described on p. 357.

Alismaceæ and **Butomeæ**. For Alisma Plantago Meyen, and especially Unger [2], have given exact descriptions of the canals with milky contents, while Frank has cleared up the history of their development. According to Unger's description the passages are absent from the roots, but are distributed throughout the rest of the plant. In the rhizome they traverse the parenchyma, forming a network branching in all directions, and with a course independent of the vascular bundles. Those which enter the petiole and peduncle branch off from this network, and then take a longitudinal course, being

[1] Botan. Zeitg. 1859, p. 333.

[2] Meyen, Phytotomie, Taf. XIV.—Unger, Das System der Milchsaftgänge in Alisma Plantago, Denksch. d. Wiener Acad. Bd. XIII. 1857.—Van Tieghem, *l. c.*

connected on the way by occasional transverse anastomoses. Those of the peduncle only occur in the hypodermal parenchyma. In the lacunar tissue of the petiole lie numerous small vascular bundles at the periphery, and five arranged in a curve in the middle. Externally to each peripheral bundle, and between it and the hypodermal layer of cells, lies one passage; one wider one, with its epithelium abutting directly on the epidermis, alternates with each pair of peripheral bundles. Around the inner bundles there is in the layer of parenchyma surrounding them, one passage opposite the points of insertion of each of the plates of parenchyma separating the air cavities. In the lamina of the developed foliage-leaves the passages appear on both sides immediately beneath the epidermis: their main trunks accompany the chief vascular bundles of the leaf: their very abundant branches together form a completely closed net, the meshes of which do not coincide with those of the network of bundles. The linear primordial leaves of the young plant have only three passages, which accompany the three vascular bundles, and only come together at the apex of the leaf. Those which enter bracts and sepals are only connected one with another at the base of these organs by anastomoses, and then run parallel towards the apex, and end blindly short of the latter.

In Sagittaria sagittifolia the passages are arranged in the cortex of the stolons in two circles, the one peripheral, the other internal, near to the cylinder of vascular bundles; in the petiole, which has a structure like that of Alisma, passages are found between the epidermis and those vascular bundles which do not abut directly upon it; there are others, which are arranged between the bundles, and singly at the points of union of the plates of parenchyma which separate the air cavities (van Tieghem).

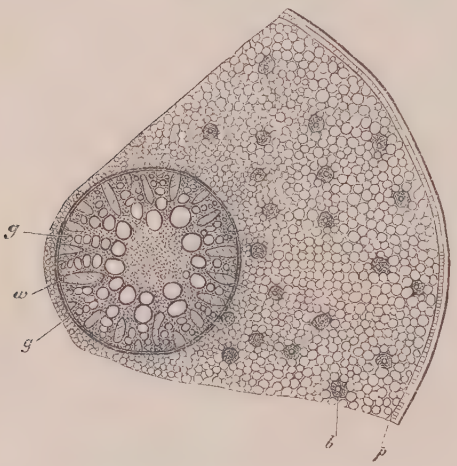

FIG. 192.—Philodendron Imbe Hort. Halens; transverse section of a strong subsidiary root, slightly magnified. Axile vascular strand, to the right the whole cortex; *g* outer margin of the xylem rows. The obliquely-shaded radial bands, *w*, are the phloem groups; *p* periderm; *b* fibrous bundle surrounding a laticiferous intercellular passage.

Similar conditions to those in the Alismaceæ described are found in Hydrocleis Humboldtii, for the details of which reference must be made to Schleiden[1] and van Tieghem. Here also the passages are wanting in the roots.

Among the *Arideæ*, according to the observations of Trécul[2] and van Tieghem[3], there are passages containing resin and ethereal oil in the genera Philodendron, Homalonema, Schismatoglottis, and gum passages in many species of Aglaonema. The other genera of the family in question, as far as investigated on this point, have no passages: this applies on the one hand to all those which have true milk-tubes, and on the other to those whose vascular bundles are accompanied neither by milk-tubes nor by rows of tannin-containing sacs, comp. p. 436. The resin passages of numerous investigated species of Philodendron traverse all the members of the plant longitudinally as narrow canals, apparently (but nothing is stated explicitly on this point) in such a way that they are all connected one with another at the nodes and other points of insertion. In the lateral roots, the stem, and petiole, they are scattered in the parenchyma, forming in the cortex of the root 3, 4–5, or even 8 (Ph. Melinoni) more or less regular concentric rows (Fig. 192);

[1] Grundzüge, 3 Aufl. I. p. 267.

[2] Comptes Rendus, tom. LXII. p. 29 (1866).

[3] Structure des Aroidées, *l.c.*

and occurring in stem and petiole either in the peripheral zones of parenchyma only, and even within the hypodermal collenchyma, or also (Philodendron hastatum, tripartitum, micans) internally, between the vascular bundles. In the leaf-lamina they run in the parenchyma between the tertiary branches of the bundles and parallel to them; either about the middle-plane of the leaf (e.g. Ph. micans, lacerum, crinipes, Imbe, &c.); or near to the lower surface of the leaf, and only separated from its epidermis by 1–2 layers of cells (e.g. Ph. eximium, Rudgeanum, Sellowianum, pinnatifidum, cannæfolium, &c.).

The passages of Schismatoglottis, Homalonema rubescens, and H. Porteanum resemble those of Philodendron in fundamental points of form and course, but with the limitation that in the stem of H. rubescens, instead of elongated canals, there are found elliptical cavities from 0·25^{mm} to 0·50^{mm} in length and 0·20^{mm} to 0·38^{mm} in width. It is remarkable that, according to Trécul's account, the canals and cavities are entirely absent in H. Wendlandii.

The parenchyma of the stem of Aglaonema marantæfolium is traversed throughout its whole length by gum- (or mucilage-) passages about 0·24^{mm} wide, which, however, are not continued into the leaves nor into the peduncle. In A. simplex these are absent.

Van Tieghem found similar gum-passages in the petiole and midrib of the leaves of Monstera surinamensis, in the cortex of the stem, and in the petiole of Rhaphidophora pinnata, and in the lower part of the petiole of Anthurium crassinervium, while they are absent in M. Adansonii, Rh. angustifolia, and Anth. violaceum.

The above-mentioned resin-passages have, as was above indicated, a typical structure; in the roots of Philodendron their epithelium, which is composed of 2–3 layers, is sheathed by 2–3 closely connected layers of narrow elongated sclerenchymatous fibres (comp. p. 202). The resin-cavities in the stem of Homalonema are enclosed by several layers of thin-walled cells arranged in radial rows (apparently derived by division from so many primary cells); the inmost project uniformly in a convex manner into the cavities. The gum-passages above mentioned are surrounded by a layer of small cells, often projecting, as in the Marattiaceæ, into the passage: these differ but slightly from those of the adjoining parenchyma.

In the rhizomes of the investigated species of *Canna*, and also in the lower portions of the flowering stems, there are numerous passages: these are filled by a clear transparent mucilage, which oozes out in glistening drops when they are cut through. The passages are absent from the cortex, and are very numerous within the periphery of the vascular cylinder: in the middle they are less frequent. They traverse the rhizome longitudinally, their endings have not been observed; anastomoses and points of branching were found here and there. Their walls are composed of small cells with abundant protoplasm, which often project as irregular papillæ into the passage. There has been as yet no thorough investigation of their development.

Among the *Compositæ*[1] all investigated forms of the section *Tubifloræ* have a system of oil passages characterised by complexity of composition and uniformity of arrangement. There are no investigations at hand concerning the *Labiatifloræ*. In the Ligulifloral Cichoriaceæ they are absent, with the exception of isolated cases to be mentioned ultimately.

In the roots of the *Corymbiferæ* and *Cynareæ* the passages lie in the innermost portions of the primary cortex, and when typically arranged they form a simple curved series opposite each phloem group of the axile vascular bundle, thus alternating with two xylem plates of the latter. According to the usual plan of structure of the roots, the cells of the inner layers of parenchyma are in these plants also arranged in regular radial and concentric rows; between the angles of junction of any set of four there is a 4- or 3-angled intercellular passage; the inmost layer has the properties of the endodermis. In the simplest case the angular intercellular passages, lying at the point indicated between the endodermis and the next outer layer of parenchyma, assume the properties (i.e. the

[1] Van Tieghem, Canaux Sécréteurs, *l.c.*

contents) of oil-containing passages. There they together form the curved series, and are separated from one another laterally by a single cell only. According to van Tieghem the oil passages, especially in Tagetes patula, arise at the point indicated, between concentric layers of cells, which are derived by tangential division of the originally simple endodermal layer, the latter remaining simple opposite the plates of xylem. In the seedling of Helianthus annuus both cases may be found side by side in the same main root. In addition to these normal passages there are not uncommonly other peripheral ones, which arise in the same way between the layer surrounding the endodermis and the next outer layer. All the passages are at first narrow, the two lateral and outermost ones of each normal curved series are triangular, the rest quadrangular. When a peripheral series is present, its members may coalesce with those of the inner series by splitting of the cell-wall separating them. The number of the passages of any normal curved series or group shows individual variations even in one and the same root, but comparison of a number of cases shows that there are different average numbers which are characteristic for groups, genera, and species.

These numbers are highest in those Cynareæ which have been investigated—the following quotations refer in each case to a single group opposite one mass of phloem;—there are 10 and more in the diarch main roots of Carduus pycnocephalus, Silybum marianum, Xeranthemum cylindraceum, the diarch or triarch roots of Centaurea atropurpurea, Echinops exaltatus; 15–20 in the diarch main root of Cirsium arvense; 12–15 in the tetrarch subsidiary roots of Serratula centauroides. Calendula officinalis has 8–10; Venidium calendulaceum 3–5.

In the Senecioneæ the number decreases; e. g. Helianthus annuus, in the tetrarch main root, 5-8[1]; Gnaphalium in the diarch root, 5–8; Tagetes patula, in the diarch main root, 5–7; Arnica Chamissonis, Tanacetum vulgare, tetrarch, 4–6; Cotula matricarioides triarch, 2; Achillea millefolium the same, 1–3; Senecio vulgaris, tetrarch, 2, sometimes united into one; Pyrethrum Parthenium, triarch, 1, rarely 3, &c.

Among the Astereæ van Tieghem found 6–8 in a triarch root of Inula montana, but only one in Bellis perennis, Erigeron glabellus, Aster, Conyza, and species of Solidago. In the latter cases, especially in Solidago limoniifolia, the canal may be greatly widened, by the separation of the cells which originally limited it externally, so that it extends as far as the next outer layer, or even continues, by further separation of cells, into several layers which lie further out.

Among the Eupatorieæ a triarch root of Tussilago Farfara showed 5–7 passages; a similar one of Ageratum conyzoides had 2–3; Petasites niveus and Eupatorium aromaticum have 1 each, which is extended as in Solidago.

As the primary cortex is stretched by the secondary formation of wood and bast, the primary passages of the root, at least in the investigated Senecioneæ, remain in their place, while they increase to a variable extent in width, and the cells surrounding them in number by division. Compare the details on Tagetes patula in van Tieghem *l.c.* and the drawing of Radix Artemisiæ in Berg. Atlas, Taf. XV.

In the stem of the Compositæ in question the oil passages are only absent in relatively few exceptional cases: Echinops exaltatus, Gnaphalium citrinum, according to van Tieghem. In by far the most numerous cases they are continuous from the root through the stem with its branches and leaves, but subject to branchings, or increase in numbers, which will be described below. They are seated in the primary tissue of the stem always in close contact with the outer side of the plerome sheath, which in the Compositæ (p. 415) may be followed from the hypocotyledonary portion through the whole stem, covering the outside of the ring of vascular bundles. In the hypocotyledonary stem the passages have the same structure and arrangement as in the root; higher up, and especially from the cotyledonary node onwards, they change their arrangement, according to that of the vascular bundles, in a manner to be mentioned immediately; they are

[1] Compare Sachs, Botan. Zeitg. 1859, Taf. VIII. Fig. 7.

separated from the plerome-sheath by a special layer, often consisting of numerous small epithelial cells. In addition to those which traverse the primary cortex, there are in certain species, but not all, other passages situated at the periphery of the pith, but these are only to be seen above the cotyledonary node.

As regards the special distribution in the transverse section of the stem van Tieghem quotes the following special cases.

(1) Only cortical passages are present in contact with the plerome-sheath.

(*a*) Only one passage in the middle of the outer margin of each main leaf-trace bundle; Senecio vulgaris, Kleinia ficoides, Cineraria maritima, Flaveria contrajerva, Bellis perennis, Petasites niveus, Baccharis halimifolia, &c.

(*b*) The same, but in addition as many passages opposite the outer margin of each united leaf-trace (faisceau réparateur) as single bundles of the trace coalesce above to form the united trace: Aster.

(*c*) On each side close to the phloem of each main bundle of the trace is one passage: Tagetes patula, Arnica Chamissonis, Tanacetum vulgare, Cotula matricarioides, Anacyclus Pyrethrum, Pyrethrum Parthenium, Santolina Chamæcyparissus, Achillea Millefolium, Zinnia elegans, Inula montana, Cirsium arvense, &c.

(*d*) An unequal number, e.g. 3–5 passages opposite the outer margin of each main bundle: Centaurea atropurpurea.

(*e*) A group of passages opposite each lateral margin of the phloem of each main bundle: Silybum marianum.

(2) Cortical and medullary passages are present, the latter opposite the xylem of the bundles.

(*a*) Medullary passages only opposite single bundles, e. g. two: Ageratum conyzoides.

(*b*) Opposite each bundle of the leaf-trace is externally a cortical, and internally a medullary passage: Solidago limonifolia.

(*c*) Opposite each bundle of the leaf-trace one medullary and several cortical passages occur: Serratula centauroides, Dahlia variabilis.

(*d*) Near each bundle is one group of medullary and one of cortical passages: Carduus pycnocephalus, Spilanthes fusca.

(*e*) Opposite each bundle is a curved series of medullary and another of cortical passages: Helianthus tuberosus.

The petioles and leaves have no oil passages when they are absent in the stems bearing them, while they are rarely wanting when the latter do contain passages: Xeranthemum cylindraceum, Cirsium arvense, radical leaves of Lappa grandiflora. In most cases oil passages are present in the leaves, and especially as direct continuations or branches of cauline passages; often also others occur which may be called accessory. The former may, however, be called fascicular, since they accompany the bundles, either directly, like the cortical ones, or in close proximity to the parenchymatous or endodermal sheath, which each individual bundle takes with it from the stem into the leaf. In single plants, as Tussilago Farfara and Cineraria maritima, they are intercalated in the sheath itself. Their number and arrangement about each bundle, as seen in transverse section, differ similarly according to the species, but still more variously than in the stem, as may be seen from the examples quoted by van Tieghem, *l.c.*, pp. 118 and 133, &c. They either accompany the branches of the vascular bundles through the lamina (on this point closer investigation is required), or they are limited to the midrib or rachis, as in the leaf of Tagetes patula, where they do not enter the lateral segments of the leaf. Their form, average size, and limitation are, at least at first, the same as in the root.

In addition to these fascicular passages there are in single cases, in those species which form passages in the secondary bast of the stem, others situated in the last-formed parts of the phloem of the petiolar bundle: e. g. Helianthus annuus.

Van Tieghem found accessory passages in the leaf of Solidago limoniifolia: beneath the epidermis of the lower surface, and separated from it by 1–2 layers of collenchymatous cells, there is a series of 3–5 narrow canals on either side of the mid-rib. Again, in

Tagetes patula: neither the cotyledons nor the lateral portions of the lamina receive fascicular passages in this plant. On the other hand there is on either side along the margin, in the parenchyma of the lower side of the leaf, an unbroken series of oil-containing (schizogenetic) sacs, closed blindly on both sides (comp. p. 201).

Finally, in the Cichoriaceæ the oil passages are wanting in all parts in most species investigated, and in the stems and leaves of all species. But in the root of Scolymus grandiflorus van Tieghem found them in groups of five, with exactly the same position, origin, and structure as the primary ones of the roots of the Senecioneæ. And in the diarch main root of Cichorium Intybus and Lampsana communis there are also rudiments of passages, there being the characteristic cell-divisions, but no opening of the passage at those points of the endodermis where they arise in other Compositæ. Scolymus is therefore the one known member of the Cichoriaceæ which really has oil passages in addition to the laticiferous tubes.

The case seems to be different with the relations between the occurrence of oil passages and that of the sacs with milky contents, which accompany the vascular bundles (comp. p. 149). At least van Tieghem found both organs side by side in the upper part of the stem and leaves in Cirsium arvense and Lappa; it is true that in the leaves the passages soon stop, and the sacs become the more numerous. The same seems to be the case in other species, e.g. according to Trécul's and van Tieghem's statements in Cynara Scolymus; but on this point further investigations are wanted.

All investigated *Umbelliferæ*[1] have without exception a very complex system of longitudinal usually anastomosing sap-passages, the contents of which are ethereal oils with resin or milky mixtures of these bodies with mucilage and solutions of gum.

In the primary tissues of the *root* the passages lie exclusively at the periphery of the vascular strand, directly within the endodermis. Their formation starts from a portion of the one-layered ring of pericambium situated in each transverse section opposite the angle of each vascular plate. The number of the cells of this portion is always even; e.g. 6, 10, 12; the radial wall, which separates the two central ones (it may be called the middle wall), is opposite the outermost vessel of the plate, in the extension of its median plane. On both sides of it lies an equal number (e.g. 3, 5 . . .) of passage-forming cells. These are at first rectangular in transverse section, and somewhat radially elongated. Each then divides into two cells by a wall, inserted at the middle of its outer wall, inclined at about 45° to the radial wall facing the elongation of the vascular plate, and meeting this further out than its middle; of these two cells one is large and irregularly 5-angled in transverse section, and one small and triangular. The triangular cells lie at the outer limit of the pericambial layer, the 5-angled cells extend through its whole thickness; the middle radial wall of the portion of the ring is met by two, all the rest by one of the inclined walls. At the angles between each triangular cell and its 5-angular sister-cell an oil passage arises by splitting of the walls; this passage is situated at the middle radial wall, and is quadrangular, being limited externally by the two originally triangular cells which remain small, internally by two 5-angled cells; at all other radial walls, however, a triangular passage is formed, limited externally by one triangular, and internally by two 5-angular cells. Opposite each vascular plate both of two- and of many-rayed bundles there arises a curved series of passages, the number of which must always be uneven: one central one and on either side of it the same number of lateral ones. The absolute number varies in species and individual between five and thirteen opposite each vascular plate. The middle quadrangular one of the passages of each group is the largest, and the width of the rest diminishes as they are further removed from it.

In addition to these passages, which correspond to the vascular plates, one smaller one appears rather later in the middle of each sieve-group. It is pentagonal in transverse

[1] Jochmann, De Umbelliferarum Structura, Berlin, 1854.—Trécul, Comptes Rendus, tom. LXIII. pp. 154, 201 (1866).—N. J. C. Müller, in Pringsheim's Jahrb. V. *l.c.*—Van Tieghem, Ann. Sci. Nat. 5 sér. XVI. Compare above, § 50.

section, and is bounded externally by two cells of the pericambial ring, internally by three cells of the phloem group. The whole number of the passages in one root-bundle may accordingly be very large, e. g. 2 × 11 next the xylem, plus 2 in the phloem, in the diarch main root of Pastinaca; 4 × 5 next the xylem, plus 4 in the phloem, in the tetrarch adventitious roots of Œnanthe pimpinelloides, &c. Adventitious roots like those of the last-named plant may retain this primary structure for a long time, or even throughout life. Usually, however, and in all investigated main roots, it is altered at an early stage. The cambium which appears in the bundle (Sect. 139) produces externally a massive, and for the most part parenchymatous secondary cortex; the primary cortex, together with the endodermis, is simultaneously thrown off with an abundant formation of periderm (sect. 176) starting from the pericambial cells lying outside the passages, and strong increase and division of the pericambial cells lying within the passages. The passages thus come to lie near to the inner side of the periderm, at first with their original arrangement, later, as the result of the increasing growth in thickness of the cortex, more and more dislocated. They then represent the canals described by Trécul, which lie under the peridermal covering of the roots of Umbelliferæ.

The hypocotyledonary stem of the seedling retains approximately the structure of the bundles and arrangement of the passages of the root till close below the cotyledons. One passage branches out from the hypocotyledonary stem to each of the three vascular bundles which enter there, and has in the cotyledon a position close to and opposite the phloem of the bundle.

Though there are no definite statements on this point, it cannot be doubted that a connection exists in the cotyledonary node between the passages hitherto described and those found higher up in the stem.

The arrangement of these differs in most cases from those hitherto treated of.

In the outer cortex of the internodes there is as a rule one passage opposite each vascular bundle, or each of the stronger ones (Fig. 193). Since one angle of the stem or one hypodermal collenchymatous bundle corresponds usually to each of the latter, especially the stronger ones, the passages are thus, as Trécul states, also opposite the strands of collenchyma. Instead of one only, 2, 3, or even 4 passages may be opposite to one broad strand of collenchyma. According to the species these passages are either near to the periphery, close to or even in the strand of collenchyma; or they have a more internal position in the parenchyma between the latter and the vascular bundle. In the creeping stem of Hydrocotyle vulgaris there is a passage, at the inner limit of the non-collenchymatous cortex, closely opposite each vascular bundle, with its epithelium directly adjoining the inner face of the endodermis (p. 121); the same arrangement appears in the branches of Bupleurum fruticosum.

In addition to the passages mentioned, which may be called fascicular, there are in many species more or less numerous ones situated in other positions in the outer cortex; thus e. g. according to Trécul, in all regions of it, from the epidermis to the limit of the ring of bundles in Smyrnium Olusatrum, Ægopodium Podagraria, and Sison Amomum. Trécul distinguishes, according to the conditions of arrangement indicated, ten types, the number of which may be increased if necessary.

Almost all Umbelliferæ have oil passages in the pith of the internodes of the stem; but Trécul cites Bupleurum Gerardi and ranunculoides as exceptions to this. Also in Hydrocotyle vulgaris and Xanthosia rotundifolia I find no medullary passages. The flowering branches of Bupleurum fruticosum show, according to the same author, in the upper internodes numerous medullary passages alternating with the inner margins of the vascular bundles; in the lower internodes the number of them diminishes successively, but they seem, according to the description, which I cannot fully understand, to be present originally also at the base of the branch, and to be crushed by secondary extension of the surrounding cells of the pith. In the seedling of Fœniculum officinale the medullary passages are often entirely absent in the first internodes (comp. Fig. 193); in higher internodes they appear quite isolated at first, but in large numbers in the stronger plant.

Where the pith is permanent, e. g. in the stems of species of Ferula and the rhizome of Imperatoria Ostruthium [1], the passages may be scattered through the whole pith. In the numerous species with internodes which become hollow they are limited to the persistent periphery of the pith (Anthriscus vulgaris, Myrrhus, Carum Carvi, Heracleum sp.) If they are originally formed in the middle, and this is a point which is not decided, they disappear with the cells of the pith surrounding them. In some cases, however, the passages persist in the middle of stems which become hollow, either surrounded by some layers of pith-cells, and standing freely and singly in the hollow (Smyrnium Olusatrum), or embedded in permanent lamellæ of pith, which extend from the periphery into the hollow (Heracleum Sphondylium).

The passages described run through the internodes as a rule with a straight, longitudinal course, and few branches or anastomoses. There are, however, numerous branches at and near to the nodes, by which all anastomose one with another, and are extended into the leaves and axillary shoots. Blind endings have not been observed. Also the sacs described in the old rhizome of Imperatoria are only huge dilatations of the passages.

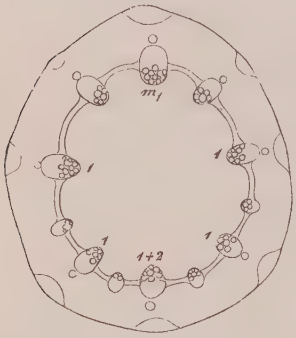

FIG. 193. — Transverse section through an internode of a young plant of Fœniculum officinale (40); pith surrounded by the partly numbered vascular ring. Between the bundles the cambium zone connecting them is indicated; the small circle outside the stronger bundles is the transverse section of an oil passage; in each of the blunt angles of the stem the transverse section of a fibrous bundle is indicated in form of a segment of a circle. Compare p. 241.

The passages have a similar distribution in the petiole to that in the stem. Anastomoses, even of reticulate form, occur at the points of insertion of the segments of divided or compound leaves. The branches finally enter the lamina. Here, according to Trécul's observations on Angelica silvestris, Opoponax, Imperatoria, Smyrnium, Ferula tingitana, Lagœcia, &c., and also in Eryngium, they accompany the vascular bundles, in such a way that they traverse the nerve both on the upper and on the under side, in the latter position they are on the average larger and more numerous; there is one in each of the smaller nerves, in the larger there are often several; further they are connected and in open communication by means of their ultimate branches so as to form a network similar to that of the bundles.

The sap-passages of the *Araliaceæ* contain resin in most cases investigated; according to Trécul they contain gum in Aralia chinensis, spinosa, Panax Lessonii, P. crassifolium, &c. According to Trécul's investigations of numerous species of the genera Hedera, Paratropia, Cussonia, and the plants already named, they are as generally distributed in this family as in the Umbelliferæ, and the general plan of their arrangement and course in root, stem, and leaves, as well as their various modifications according to single species, correspond so closely to those in the Umbelliferæ, that they need not be thoroughly entered into here, but reference may be made for many details to Trécul[2] and N. Müller (*l.c.*). In the roots of Hedera Helix and Aralia Sieboldtii van Tieghem found the number and arrangement of the primary groups near the vascular plates to be not always so very regular as in the Umbelliferæ, and those in the phloem to be either in contact with the pericambium, or completely enclosed in the phloem. The numerous anastomoses between the radially undulated passages of the primary (and also secondary) cortex of the branch of Paratropia macrophylla observed by Trécul may here also be mentioned, and the statement of the same author, that in the lamina of Panax Lessonii and crassifolium the passages seem to occur in the mid-rib only, and apparently do not follow the lateral branches of the vascular bundles.

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[1] Compare Berg, Atlas z. Pharm. Waarenkunde, Taf. 22.—Wigand, Pharmacognosie.

[2] Des Vaisseaux propres dans les Araliacées; Comptes Rendus, tom. LXI. p. 1163 (1865).

The family of the *Clusiaceæ*[1] has especially numerous passages containing gum-resin, and in fact all members of it with exception of the genus Quiina, which is separated as a special group.

According to Trécul's and van Tieghem's investigations there are in the stem and roots of the true Clusiaceæ three chief forms of distribution of the passages. In the genus Clusia they lie only in the primary parenchyma, in the stem they occur also in the pith, but are absent from the vascular bundles and the secondary cortex.

A second category has passages in the phloem of the vascular bundles in addition to the above-mentioned places; there being one in each primary phloem-group of the root-bundle, in each primary bundle of the stem, and further in the secondary bast; e. g. Mammea americana: the same distribution, with the exception of those in the primary bundles of the stem, is seen in Calophyllum Calaba.

Thirdly: the passages are wanting in the cortical parenchyma of the root, but are present in that of the stem, and in the primary phloem-groups and the secondary bast both of the root and of the stem: Rheedia lateriflora, Xanthochymus pictorius. They are present in the pith of the stem in Rheedia, but not in Xanthochymus.

The passages run longitudinally and anastomose one with another through the whole plant: more rarely in the internodes, but always, and in various individual forms described by Trécul, in the nodes. From the latter, branches of the passages go into the petiole, and through this further into the lamina. In these members they are found in most species only in the parenchyma and the watery hypoderma. Only in Mammea americana a number of the vascular bundles entering the petiole take the passage which traverses their phloem with them out of the stem: in the case of the median bundle it goes nearly to the apex of the leaf. The number of those which enter the petiole is usually high, and varies according to species. Trécul states, e. g. that there are 30 in Rheedia lateriflora, about 40 in Xanthochymus pictorius, 14–20 in Calophyllum Calaba, and more than 200 in Clusia rosea. Their distribution in the parenchyma varies according to the species. Finally, in the lamina also they run without relation to the vascular bundles, even crossing these in certain cases, and branched here and there, but without visible anastomoses. According to the arrangement in the massive leaf-substance there may be distinguished a system of internal passages situated with vascular bundles in the inner chlorophyll parenchyma, and a hypodermal system, of which the passages are always narrower. For details on these relations see Trécul, *l. c.* Of the forms investigated Mammea americana alone has no passage in the lamina except that which traverses the mid-rib, but has instead a round resin-containing cavity embedded in the parenchyma in each mesh of the network of vascular bundles.

Pittosporeæ[2]. The *root* of Pittosporum Tobira shows originally opposite each vascular plate a group of oil and resin passages of similar origin and arrangement to those in the Umbelliferæ. The number of the passages in each group is certainly smaller, and their arrangement often less regular than in this order: there is a central quadrangular one, and usually on either side of it a smaller, triangular one. The passages in the phloem-strands are absent in Pittosporum. By the same process of secondary formation as in the Umbelliferæ the passages are subsequently pushed outwards, under the periderm, while they widen considerably, and the cells limiting them increase in number. In the primary tissue of the *stem* there is only one passage in the outer part of the phloem of each vascular bundle, and these passages of the stem are continuous with those of the root at the limit of the two members. The bundles which enter the leaf are each accompanied by one passage, which retains the same position as in the stem, and divides in the lamina into branches, which also follow the branches of different rank of the vascular bundles.

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[1] Meyen, Physiol. II. p. 384.—Anonymous author in Botan. Zeitg. 1846.—Trécul, in Comptes Rendus, LXIII. pp. 537 and 613 (1866).—Van Tieghem, *l. c.*

[2] Müller, *l. c.*—Van Tieghem, *l. c.*

The same conditions of arrangement as in Pittosporum are found in the primary vascular bundles of the branches and leaves of Sollya heterophylla, and Citriobatus multiflorus. Bursera spinosa, however, never has sap-passages, according to van Tieghem.

Cacteæ. The passages containing latex in many *Mamillariæ* (comp. pp. 202, 206) traverse the whole stem, and are scattered through the parenchyma. They are rare in the inner pith, but numerous in the zone of parenchyma situated between the ring of wood and the inner circle of cauline bundles (comp. p. 254), in the whole cortex, and the mamillæ. They are branched in all directions, and all branches communicate openly one with another; those which enter the mamillæ run within them near to the axile strands of xylem, and give off numerous branches, which are repeatedly branched and run through the chlorophyll-parenchyma straight towards the surface, many of them as far as the simple hypodermal layer of collenchyma.

In other Cacteæ these passages are not found. Those found by Schleiden[1] in *Opuntia* peruviana differ fundamentally from them. I have investigated them in O. robusta. They lie here close to the outer limit of the phloem (not, as Schleiden states, in it) of the bundles of the trace, which are connected into a net, and follow them in their longitudinal course. They are apparently of lysigenetic origin, being cavities in the parenchyma, which attain a width of $\frac{1}{2}$ mm, and are filled with swollen, sometimes still recognisable cells, and numerous conglomerated crystals of calcium oxalate embedded in the mucilage.

The investigated *Anacardiaceæ*—Schinus molle, Spondias cytherea, Pistacia vera, Lentiscus, Rhus aromatica, suaveolens, Cotinus, Coriaria, virens, Toxicodendron, typhina, glauca, elegans, semialata[2], and villosa—are, as regards the disposition of their passages containing mixtures of gum-resins, distinguished by the fact that they are situated in the stem and leaves in the phloem of the primary vascular bundles. Further, in addition to this, there are others in the secondary bast of the stem, from which, in Rhus viminalis, blindly ending branches penetrate here and there horizontally into the medullary rays of the xylem: finally, in many species (Rhus toxicodendron, typhina, glauca, elegans, viminalis, semialata, and Spondias cytherea) there are medullary passages.

In the root a relatively large passage lies in the middle of each phloem portion of the primary, usually 2 or 3 rayed vascular bundle. In the secondary layer of bast new ones are successively added.

The phloem portion of the primary bundles of the stem is limited from the parenchymatous outer cortex by a strong bundle of sclerenchymatous fibres of half-moon shaped transverse section, and the fibrous bundles are almost in contact with one another at their margins, thus forming together a ring surrounding the outer cortex. Outside this there is no resin passage, but there is a thick one immediately within it in the phloem of each bundle. In the secondary cortex, which appears later internally, new ones are formed successively in the strands of bast. The medullary passages vary in number, according to the species; Trécul gives as the number, e. g. in a transverse section of a branch of R. semialata 58, typhina 25, viminalis 5–12; the larger number are situated especially at the periphery of the pith, the minority scattered irregularly. According to successive transverse sections it appears that a part at least of the medullary passages ends blind in the pith. The cortical passages, as far as they belong to the secondary bast, are connected also in the internodes by more or less numerous tangential anastomoses. In the nodes the cortical passages anastomose both with one another, and also with the medullary passages by means of branches, which follow the vascular bundles out into the leaf; from the plexus of anastomoses the passages are continued down into the next internode and into the leaf.

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[1] Anatomie der Cacteen (Mém. prés. Acad. S. Pétersbg. tom. IV), p. 358, Taf. VII. 4.

[2] Trécul, Des Vaisseaux propres dans les Térébinthinées. Comptes Rendus, tom. LXV. p. 17, 1867.—Van Tieghem, *l. c.*

The branches observed by Trécul in Rhus viminalis, which pass into the wood, pass off nearly at right angles from the cortical bundles, and into the medullary rays, without reaching the medullary passages.

The vascular bundles passing into the petiole, which are arranged in curves in its transverse section, and branch in their further course, take with them one passage each from the stem: these passages have the same position as those in the primary bundles. The same is the case with the stronger branches of the bundles, while the passage is often absent in the weaker ones. In addition to these passages there are in the petiole of Rhus semialata medullary passages also, which lie 1–3 together on the inside of the strongest bundles; in the petiole of Spondias cytherea one is placed opposite the inner margin of the median bundle. A similar arrangement, the details of which may be read in Trécul's work, is found in the mid-ribs of leaves and leaflets; these contain several vascular bundles, which turn their phloem, and also the resin-passages sometimes towards the upper, sometimes towards the lower surface of the leaf. All lateral ribs contain but one passage turned towards the lower surface of the leaf, and even this is absent from the last branches of the bundles. In Rh. semialata and glauca Trécul saw the passages of the leaf-lamina anastomosing in a reticulate manner like the vascular bundles, which they accompany.

According to van Tieghem's investigations of Bursera gummifera, and the transverse sections of branches of species of Balsamodendron and Protium figured by Marchand[1], there is found in these balsam-bearing trees of the order *Burseraceæ* a structure of the cortex similar throughout to that described in the Anacardiaceæ, and the same distribution of the gum-resin passages in the roots, the stems and their branches, and the petioles.

In the genera *Ailantus* and *Brucea*[2], now placed among the *Simarubeæ*, there are longitudinally-running sap-passages, as in many species of Rhus, at the periphery of the pith of the stem; in Ailantus glandulosa as many as 60; in other regions of the stem they are wanting. They appear, according to accounts at hand, to traverse the successive internodes, and to give off branches at the nodes into the leaves; this is not, however, distinctly stated. At all events the passages are again found in the petioles and the mid-rib of the leaflets, and in the pith-like parenchyma surrounded by vascular bundles arranged in curves or rings, or lying between these. They are not present in the lateral ribs which are given off from the mid-ribs of the leaflets.

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[1] L. Marchand, Recherches pour servir à l'histoire des Burseracées; in Baillon, Adansonia, tom. VII. p. 258, pl. VIII, et tom. VIII, pp. 17, 74, pl. II., III.

[2] Trécul, Vaisseaux propres des Térébinthacées, *l. c.*

SECOND SECTION.

SECONDARY CHANGES.

CHAPTER XIV.

SECONDARY GROWTH IN THICKNESS OF NORMAL DICOTYLEDONOUS STEMS AND ROOTS.

I. Cambium. General Arrangement of the Secondary Thickening.

Sect. 134. In the Dicotyledons possessing an axial bundle, in the anomalous forms enumerated on p. 250, sub. 2, in the Berberideæ and Ranunculaceæ mentioned on p. 249, and in the Peperomiæ (p. 249), the primary arrangement of the vascular bundles and of the tissues surrounding them in the *stem* undergoes no change after extension is complete.

The same statement applies to a relatively small number of forms, the stem of which possesses a normal ring of bundles, consisting of collateral leaf-trace bundles of normal orientation, as in Saurureæ, and species of Ranunculus.

In the very great majority of Dicotyledonous stems, on the other hand, the completion of the primary groups of tissue is followed by the formation of new additional elements, in consequence of which secondary changes occur in the pre-existing, primary tissues (Sect. 54, p. 224).

These changes proceed from the ring of bundles, and that is the case both in the typical instances where the latter alone is present, and also in other cases where, besides this, medullary and cortical bundles occur. The changes in question consist chiefly in the fact, that from a meristematic zone, called the *Cambium* or *Cambial ring*, which passes through the ring of bundles, new elements are added to the latter in the direction of the transverse diameter of the stem, which thus receives a (secondary) *growth in thickness*, through the addition of new elements. In short-lived stems this growth may soon cease; in long-lived ones, and especially in 'woody' plants, it endures throughout life.

As these changes go on, the number and arrangement of the primary leaf-trace bundles, and of the primary medullary rays which separate them, either remain as they were originally, or new bundles, the *Intermediate Bundles*, separated by medullary rays, appear between the original ones, their appearance sometimes immediately succeeding the primary differentiation of tissues, sometimes occurring later.

Apart from the numerous modifications of detail which thus become possible, the origin and position of the Cambium, and the arrangement of the elements pro-

duced from it, which constitute the secondary thickening, are in the main outlines the same in the very great majority of stems of Dicotyledons and Gymnosperms. The phenomena belonging to this category, to be treated of in the present Chapter, may therefore be termed those of the *normal growth in thickness*, and the stems in question be termed the normal stems, while those showing a different behaviour may be contrasted with them, as *anomalous* forms (Chap. XVI).

1. The *origin* of the Cambium takes place in cases without simultaneous or previous formation of intermediate bundles, in the following manner. The delicate cells arranged in radial rows, lying on the internal border of the phloem of the leaf-trace bundles (p. 325), remain meristematic; divisions by means of tangential walls

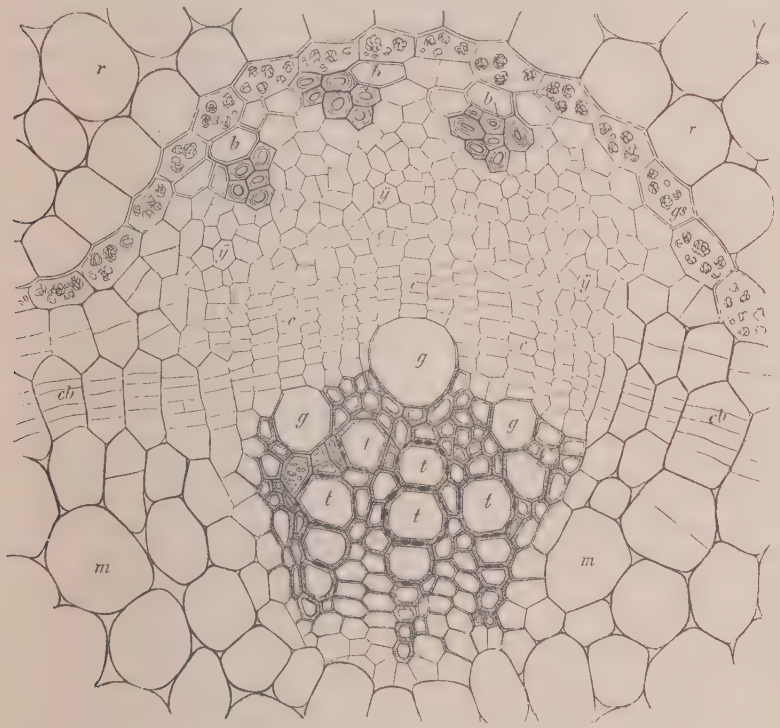

FIG. 194.—Cross-section through the fully elongated hypocotyledonary stem of Ricinus communis. *t g y* leaf-trace bundle; *c*, *c b* cambial zone; *c b* interfascicular segments of the latter, arising by tangential division of the parenchyma of the medullary ray. For further explanation compare p. 332. From Sachs' Textbook.

go on in them in the succession to be described below, and the vascular bundle thus grows in the radial direction. Sooner or later the tangential divisions are continued from the lateral edges of the phloem-groups, through a band in each medullary ray connecting these groups with one another, so as to give rise to a meristematic zone in this band also. (Comp. Fig. 194.) The meristematic annular zone, which is thus formed from the bundles, and from the segments belonging to the medullary rays, is the cambium. If the leaf-trace bundles in any cross-section are of unequal thickness, the interfascicular completion of the cambium begins at the edges of the thickest,

and then extends, in succession, to those which are less thick. In addition to the example represented in Fig. 194, the process described occurs in the Menispermeæ, Casuarinæ, and Begoniæ investigated, in Berberis and Mahonia[1], in Aristolochia Sipho and its allies, Atragene, and the woody Piperaceæ. Cucurbita is also to be mentioned here, in so far as the two concentric rings of bundles in its stem (p. 248) behave, as regards the relation in question, as a single ring curving alternately inwards and outwards.

In Cucurbita, as well as in Aristolochia Sipho and Atragene, the behaviour described is most clear, because it goes on especially slowly. In the former plant particularly the growth in thickness by means of meristematic new formation first goes on in the vascular bundles alone, the cells of the parenchymatous medullary rays following it for a long time only by means of radial extension; only at a relatively late period does tangential division begin in the latter, in the order described.

2. No doubt in the majority of cases, the first appearance of the cambium is immediately preceded by the formation of *cauline intermediate bundles*, and this happens as follows:—

(*a*) In the broad medullary ray between two leaf-trace bundles, distinct collateral vascular bundles appear, which are again separated from the leaf-traces by distinct medullary rays. The formation of the cambium then starts from the two kinds of bundles, in the same way as in (1). This process takes place in a very evident manner in the internodes of Clematis Vitalba. When the completion of the six leaf-trace bundles (p. 244) has begun, an intermediate bundle appears between each two of them in the usual manner (p. 389). The twelve bundles of the ring which are then present are separated from one another by the same number of radial bands, each about ten cells broad. The cells of the latter now assume parenchymatous properties, while the twelve vascular bundles increase and develope their elements in the radial direction; finally, the completion of the cambial ring takes place by means of tangential division of an interfascicular layer of cells, starting from the edge of the six leaf-trace bundles. Each intermediate bundle runs longitudinally through the entire internode, and is only attached by its ends to the trace-bundles, in the nodes. A further case, belonging to this category, and characterised by the very early appearance of the intermediate bundles, is represented by the Rhipsalideæ with winged corners to the stem, spoken of at p. 261.

How far the same process takes place elsewhere in internodes is not certainly known at present; the 'complementary bundles' of Ephedra campylopoda, noticed above at p. 247, may belong to the same category. It at any rate occurs very generally in the nodes, even among forms belonging to category 1, in order to form the oblique or reticulate connections of the trace bundles, which here appear in all cases at an early period.

(*b*) Between each two leaf-trace bundles collateral intermediate small bundles of normal orientation appear, consisting only of one or a few radial rows of elements, and separated both from the leaf-trace bundles and from one another by equally narrow, non-equivalent radial bands (parenchyma). Their longitudinal

[1] Sanio, Botan. Zeitg. 1863, p. 373.

course is undulated in such a manner, that within the internode they show alternately lateral union and separation, at short vertical intervals, both with one another and with the leaf-trace bundles, and thus form a net with vertically elongated, narrow meshes, which are filled up by the bands of parenchyma. The whole process begins at the lateral margins of the leaf-trace bundles, and is continued from the latter through the interfascicular segments of the original ring. It may therefore be said, that the leaf-trace bundles coalesce, by means of successive increase in breadth at their lateral margins, so as to form a closed ring, which is only traversed by the narrow radial bands of parenchyma, and in which the primary leaf-trace bundles only remain characterised by the fact that they project more deeply into the pith (and by the special structure of this projecting portion). In the typical cases, the whole body thus formed may actually be termed one collateral vascular bundle, with an annular cross-section. The origin and orientation of the cambial zone is, in the cases in question, essentially the same as in those brought forward above.

This coalescence of the leaf-trace rudiments to form a ring appears most clearly in those internodes which contain only a few trace-bundles, with a simple course. In the internode of Euonymus latifolius[1] the rudiments of the traces of the adjoining pair of leaves, each consisting of a single bundle, appear first at two diametrically opposite points, between the pith and external cortex, then the traces of the next higher pair appear in the middle of the spaces between the first. From the lateral margins of these four bundles, according to their order of origin, rapidly succeeding divisions extend through the interfascicular bands, so as to form the small-celled rudiment of the closed ring of bundles; and finally the formation of the definitive tissue takes place in the latter, beginning with new divisions and consecutive differentiation at the points where the formation of the ring started, and advancing towards completion in the same direction as the latter. The whole ring, including the original leaf-trace rudiments, consists finally, especially in the xylem, of alternating radial bands of bundles, and of non-equivalent elements, which show the longitudinal course already stated. Fraxinus[2] behaves quite similarly, and most Rubiaceæ, Asclepiadeæ, Apocyneæ, &c., having a very regular radially arranged ring of wood, are also connected with this type. Comp. Sects. 61, 63.

The formation of the closed ring is less evident in the case of internodes possessing numerous leaf-trace bundles, which from the first are separated by very narrow interfascicular bands, e. g. Acer, Sambucus[3], &c.; the result, however, is essentially the same. How far the closing of the ring proceeds exclusively from the coalescent margins of the leaf-trace bundles, or also from small intermediate bundles arising like those of Clematis, remains to be investigated for each particular case.

(*c*) The coalescence of the vascular bundles to form a continuous ring may go still further, so that no alternating dissimilar radial bands appear between the original bundles, but the whole of the tissue forming these zones assumes the structure of a vascular bundle, if this expression be allowed for the sake of brevity; i. e. it consists of the elements of vascular bundles, with similar structure and arrangement to those of the later developed portion, and of the products of secondary growth in

[1] Sanio, Botan. Zeitg. 1863, p. 360.

[2] Compare Nägeli, Beitr. 1. p. 95

[3] Ibid. *l. c.*

the bundles of the trace. The descriptions which follow below will explain this in greater detail. The formation and orientation of the cambial zone are once more the same as in other cases. Hartig[1] and Sanio state that this condition exists in the case of Ephedra monostachya, Cheiranthus Cheiri, and Mühlenbeckia complexa, Hieracium, Pyrethrum, Galium, Plantagineæ, and other plants to be mentioned immediately. I find it in Cobæa, Crassulaceæ[2] (Sedum spec., Sempervivum arboreum, Echeveria pubescens), Caryophylleæ[2] (Dianthus plumarius, Silene italica), Rumex lunaria, Campanula Vidalii, Lobelia syphilitica, Xanthosia rotundifolia, and Centradenia grandifolia. Many other Melastomaceæ, and, according to Chatin's[3] description, the Rhinanthaceæ also, appear to behave in the same way, but here it is not admissible to draw any certain conclusion from one or the other species, as to the behaviour even of its nearest allies; thus, for example, Rumex alismifolius, in contradistinction to the R. lunaria just mentioned, possesses the structure given under (*b*). Comp. also below, Sect. 147.

Sect. 135. According to the traditional terminology, the part of the ring lying on the inside of the cambial zone, and including in itself the whole of the xylem groups, is called, in stems of the Dicotyledonous type, the *wood* or *ligneous body* (*xylem* of Nägeli), while everything that lies outside the cambial zone is called the *cortex*. The latter is divided into the *bast zone*, *bast* or *liber*[4] (phloem) which, limited internally by the Cambium, includes and is characterised by all the phloem-groups of the ring, and the *external cortex*[5], Duhamel's Enveloppe cellulaire, lying outside this. In the ligneous body the elements of the vascular bundles form *strands* with the arrangement described, *wood-strands*; the bast has similar *bast-strands*, corresponding in their arrangement to the wood-strands; or, if one will, the two may be termed xylem and phloem *strands*. The bands of non-equivalent tissue—consisting in the great majority of cases of parenchyma—lying between the strands, and having a radial course, as seen in cross-section, are called *medullary rays*. Each of the latter consists of a portion belonging to the ligneous body, the medullary-ray of the wood ('Markstrahl katexochen' of Nägeli), and of a portion lying in the bast-zone (cortical medullary-ray, cortical ray of Nägeli). Those medullary rays which are formed on the first origin of the woody ring pass through from the pith to the external cortex. They have accordingly been termed *large* medullary rays, in contradistinction to those which arise later, and do not reach the pith, and are thus in this respect *smaller* rays. With reference to their origin at the first commencement of the woody ring, the former have also received the name of the original, primary rays.

The genetic relations which are indicated by the latter term are not, however, the same in all cases for the anatomically similar large medullary rays, as follows from what has been stated above. In the case described under (1) they are identical with the original rays, and thus the expression primary medullary rays is appro-

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[1] Botan. Zeitg. 1859, p. 94.

[2] Regnault, Ann. Sci. Nat. 4 sér. tom. XIV. p. 87.—Hartig, *l.c.*

[3] Anat. Comparée, p. 221.

[4] 'Liber, seu interior corticis amictus, ligno contiguus, fibris reticulatis . . . . compositus.' Malpighi, Anat. Plant. cap. I.

[5] Compare above, p. 236.

priate, according to the strict sense of the words. In the condition described under (2) (*a*) and (*b*), on the other hand, the large medullary rays have originated secondarily from the primary ones, primary rays in the sense of the first case having no more existence after the completion of the ring of wood. The plants mentioned under (2) (*c*) have, according to what has been said above, neither large nor primary medullary rays; those which appear later in the wood of Ephedra are all small ones not reaching the pith.

The cambial zone, finally, is divided into portions belonging to the strands and to the medullary rays, into *fascicular* and *interfascicular* portions, according as it borders on a medullary ray or on a strand of wood or bast.

For Sanio's terminology, which differs from the above, and the employment of which would seem to be attended with almost insuperable difficulties, comp. Bot. Ztg. 1863, p. 372.

In the cambial zone growth in the direction of the radii of the cross-section of the stem goes on, with pauses in winter; growth is followed by corresponding cell-divisions; of the products of division those bordering on the wood and bast are in each case added to these as definitive tissue; a zone lying between the two, however, remains meristematic, and from this the process of new formation is repeated.

The masses of tissue which are added by this process to the wood and bast are the *secondary* wood, and the *secondary* bast.

In the normal Dicotyledonous type, the differentiation of the two in the entire secondary growth remains essentially the same as, or at any rate quite similar to, that of the ring of bundles immediately after the first formation of the cambial zone and the intermediate bundles. On the side of the wood, new elements, equivalent to the first, are constantly added to the existing medullary rays, in their original direction, in such a manner that in absolute dimensions and number of cells they either maintain everywhere the same height and breadth, or, as they extend in the radial direction, they increase gradually, and usually relatively little, in breadth; the latter is the case especially in broad many-layered medullary rays, as in the stem of Quercus, Casuarina, Clematis, Atragene, &c. The entire ligneous body accordingly remains divided into the same number of *main strands* or *main sections* as that of the strands existing between the large medullary rays, on the completion of the ring; and these strands become successively broader towards the outside, being wedge-shaped as seen in cross-section. On the one hand, they consist as before of elements equivalent to their original ones, and the differences successively appearing in them are to be described below; on the other hand, radially-arranged plates of non-equivalent tissue occur within the strands, which are essentially similar to the large medullary rays in structure and direction: there are the *small, short, secondary* medullary rays, which sever the main section or strand into *partial sections*. In each successive zone of secondary growth new small medullary rays appear, each of which however, when once started, grows on in the radial direction, like the first medullary rays. Every main section of the wood is therefore divided up by medullary rays, which become successively more numerous and successively extend less deeply towards the pith.

On the cortical side completely similar conditions obtain to those in the wood;

the bast-zone continues to be divided into main sections by the large medullary rays, which at the boundary of the cambium are continuously increased by equivalent elements, and here for the time being show the same breadth as in the wood; each of these main sections is divided into partial sections by secondary, successively smaller medullary rays, which are a prolongation of those of the wood. The equivalent rays and sections of the wood and bast fit one on another at the cambial boundary; the younger rays, which in the wood penetrate less deeply towards the pith, penetrate to a lesser distance outwards in the bast; the wedge-like widening of the portions of the strands is necessarily in the opposite direction in the bast to that in the wood, as seen in cross-section. From this distribution, slight deviations, still to be included under the normal type, occur here and there. As such are to be mentioned—

(*a*) The *discontinuous medullary rays* of Hartig[1]. In Fagus and in exotic woods certain medullary rays in the wood do not extend to the border of the cambium, but end externally within the ligneous strand. It remains, however, to be investigated, whether this phenomenon, which appears on examining cross-sections through medullary rays of no great height, always depends on an actual termination of the ray, and a formation of bundle-elements at its exterior limit, or whether it may not perhaps be due to a vertical upward or downward curvature of the ray, in consequence of which its radial prolongation comes to lie in a different surface of cross-section from that through which the knife has passed, and in which the inner portion lies.

(*b*) The *medullary spot*, characteristic of many woods, which will be described below.

(*c*) The appearance of *secondary intermediate bundles* arising from the cambium, inside the older medullary rays. This phenomenon occurs in the internodes of Atragene alpina in a form which quite agrees with the normal processes, especially in the allied species of Clematis. In the specimens investigated the internodes in their first year all showed the six leaf-trace bundles only, distributed as in Clematis (p. 244), separated by six large medullary rays, and, like the latter, furnished with secondary growth by means of a zone of cambium extending all round the stem. In some of the older internodes, at least two years old, this structure is permanently maintained, while the secondary growth continues; they thus correspond to the type given above under 1. In others, however, intermediate bundles appear, in or after the second year, and in fact, in the most regular case, one appears on each side of each median bundle of the trace, so that the total number of the bundles now amounts to ten. In many cases one, two, or three of the four intermediate bundles are absent, and the total number of bundles is accordingly nine, eight, or seven. The longitudinal course of the intermediate bundles is that given in the case of Clematis; in one case only two of them occurred between two trace-bundles, in a short internode; they anastomosed with each other irregularly in their undulating course. The structure and subsequent growth in thickness of the intermediate bundles are similar to those of the six trace-bundles.

Clematis Vitalba frequently shows a similar phenomenon, so that in the twelve

[1] Botan. Zeitg. 1859, p. 94.

large medullary rays, or in some of them, small intermediate bundles subsequently appear, which have an undulating course[1]. Here, however, the process appears to be rare; I could not find it in my material, even in stems an inch thick. In the broad medullary rays of the wood of Casuarinæ the formation of secondary intermediate bundles seems to occur constantly, and therefore, strictly speaking, separates the stems in question from the normal Dicotyledonous type[2]. The inner, oldest portion of these bundles extends vertically, without interruption, through the whole internode. After some years intermediate bundles appear further outside, which are at first very small, but constantly become thicker as secondary growth goes on, and these frequently anastomose with one another and with the neighbouring main bundles, in an irregularly undulating course. In the older wood, even in branches one inch thick, the space corresponding to the original medullary ray is divided up by an irregular net, with pointed meshes, of small bundles. Menispermum canadense presents the same phenomenon in a less conspicuous degree. To what extent similar bast-bundles, corresponding to the secondary bundles of wood may occur, still remains to be investigated.

Sect. 136. When once formed, the cambial ring constantly increases in thickness and circumference, while successive reciprocal differentiation of wood and bast goes on. The growth of the transverse diameter of its individual cells takes place in a much smaller degree than the general growth, though in many cases they show an increase within definite limits. On the other hand, a continual increase of the number of cells goes on, by division of the existing ones. The general growth, the divisions, and the differentiation of the products of the division in the direction of wood and bast, proceed during the periods of active vegetation; they cease during the periods of rest in winter. The course of the successive divisions and differentiations is obviously only to be determined by investigation during the period of vegetation, especially at its commencement. In order to test and confirm the result thus obtained, a comparison of the resting stage in winter is of service.

In order to explain the general course of the divisions, we may, in the first instance, consider the transverse section alone, and assume that the cambial layer, as well as the immediately contiguous youngest layers of wood and bast, consist of entirely similar cells, ranged in radial rows; this assumption applies with tolerable exactness in the case of the bundles of the wood.

The following rule was first established by Sanio[3] in the case of Pinus sylvestris. (See Fig. 195.) All cell-division proceeds from a single, annular, meristematic layer of cells, one row thick as seen in cross-section, which may be called the *Initial layer*. In this every (initial) cell divides by a tangential longitudinal wall into two daughter-cells, one of which once more becomes an initial, while the other becomes a *tissue mother-cell;* the latter change may happen either to the inner of the two daughter-cells, which is added to the wood, or to the outer, which is added to the bast. In the quite regular case of Pinus sylvestris, each tissue mother-cell then divides once by a tangential wall, and the two products of its division become directly converted

[1] Compare Sanio, Botan. Zeitg. 1863, p. 127.
[2] Göppert, Linnæa, XV. (1841), p. 747, Taf. IV. Fig. 7.—Sanio, *l. c.*
[3] Pringsheim's Jahrb. Bd. IX.

into elements of the tissue. But even here, in the case of Pinus sylvestris, deviations from the latter rule may be demonstrated. Of the first products of division of the tissue mother-cell, one divides once more before passing over into definitive elements of the tissue: in the case of the wood this is always the outer one; in the case of the bast it is usually the inner, more rarely the outer; or each of them divides once more. Thus in the former case three, in the latter case four elements of the tissue are derived from one tissue mother-cell.

The investigation of good transverse sections through the active and the resting cambial zone of the most various Dicotyledonous and Coniferous woods confirms Sanio's main result, obtained in the case of Pinus sylvestris, as regards the *bundles of the wood* (comp. Figs. 196, 197). In every radial row there is one initial cell, dividing tangentially, from the division of which a new initial cell and a tissue mother-cell proceed in each case. After one or two further divisions of the latter, the definitive elements of the tissue are formed. From what is known of Pinus sylvestris, very various differences of detail as regards the divisions by which the latter elements are produced are to be expected as soon as more extended minute investigations of this difficult subject have been undertaken.

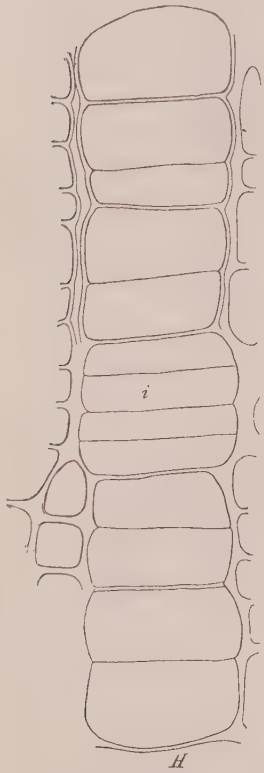

FIG. 195.—Pinus sylvestris; cambial zone; cross-section through a radial row; after Sanio (650). *H* side towards the wood, *i* (conjectural) cambial initial cell. On the side of *i* towards *H* are twin-cells of the wood; on the side of *i* towards the bast are twin-cells of the bast; the cell bordering on *i* towards the bast is the still undivided tissue mother-cell for the bast, if the interpretation of *i* stated above is correct; otherwise the former is the initial, and *i* an as yet undivided tissue-mother-cell for the wood.

In most of the cases investigated the longitudinal divisions in the tissue mother-cells take place exclusively in the tangential direction, the elements of the tissue are therefore always originally arranged in radial rows, and deviations from this rule are the result of subsequent displacement. Exceptions, however, occur in the bast of many plants, on the origin of the sieve-tubes; here the mother-cell of a member of the latter is divided by one or more excentric walls, directed neither radially nor tangentially, into a member of a sieve-tube, and cambiform cells. Comp. p. 324. This no doubt applies to all the numerous cases of irregular grouping of the sieve-tubes; it is, however, undecided how far displacements occur here, in consequence of subsequent longitudinal growth of the elements, which might give rise to the same result in the arrangement of the latter.

The variations mentioned in the differentiation and division of the tissue mother-cells are sufficient to show that the initial cells of a cambial ring do not always fit exactly one on another with their radial surfaces, and that even the equivalent products of their divisions in the entire series of radial rows form with one another annular zones which are not smooth, but are often interrupted. Comp. Fig. 196, and Sanio, *l. c.*, Taf. 5–8. In addition

to this, even casual observation shows that the secondary growth on the side of the wood is almost always far more abundant than on the side of the bast.

Both the successively developed elements of the wood and bast, and the cells of the initial layer, in certain cases, increase for a time in size, while growth in thickness proceeds, as will be described in greater detail below; from a definite period onwards, however, a constant average size is assumed by all the elements which arise subsequently, while in other cases the average size remains approximately equal from the beginning.

The number of elements in the tangential zones, and hence the number of radial rows, must therefore be constantly increased as growth in thickness proceeds,

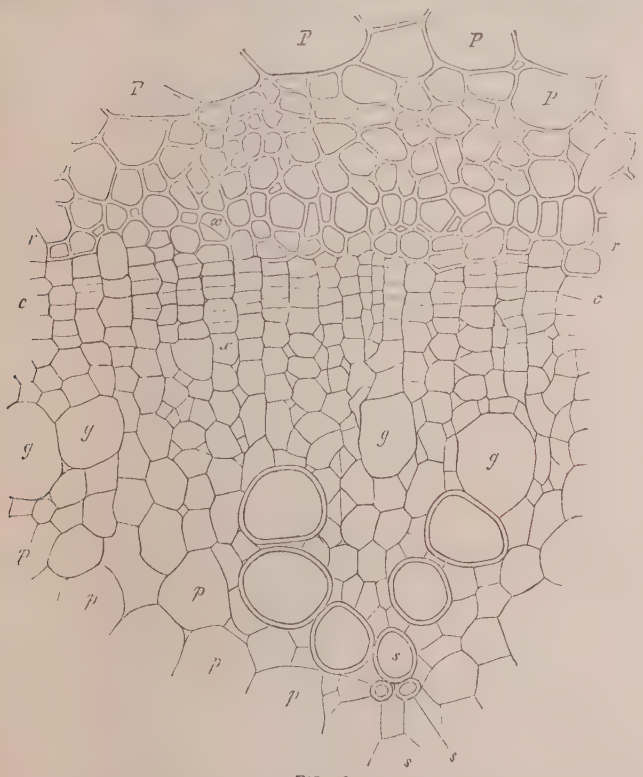

FIG. 196.

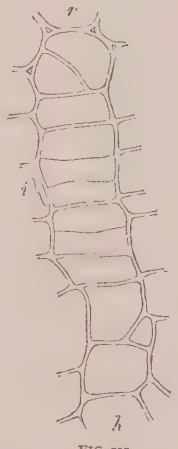

FIG. 197.

FIG. 196.—Sambucus nigra; young internode; cross-section (220). *P*, *P* limit of the parenchyma of the external cortex. Between *P*—*P* and *r*—*r* primary zone of bast (phloem); *c* cambial zone; *g*, *g* (pitted) vessels in process of formation; *p*—*p* parenchyma of the pith. The cross-sections with a double outline, at and above *s*, are the spiral vessels of a leaf-trace bundle.

FIG. 197.—The radial row *x*—*x* from the cambial layer of Fig. 196 (600); *i* seems to be the cambial initial cell, just divided; *h* side towards the wood; *r* side towards the cortex.

and this takes place by means of radial divisions of the initial cells into two equivalent daughter-cells, which then perform the functions of initial cells in the manner described. Assuming that the woody cylinder within the cambium undergoes no further enlargement, and that all the secondary elements successively formed are of equal size, it is shown, by a simple theoretical consideration[1], that for each radial

[1] Nägeli, Dickenwachsthum des Stengels, &c., bei den Sapindaceen, p. 15.

row to divide once into two, it is necessary that as many new elements should be formed in the radial direction as are already present on the radius of the cambial ring. 'An equal increase in the radial and tangential directions, so that two outer cells would correspond to every inner cell, could only take place if the diameter of the cell were equal to the radius' (i. e. only in the innermost layer of cells of a stem assumed to be destitute of pith). 'When the radius of the cambial ring has the length of 50, or 100, or 1000 wood-cells the radial rows must be prolonged by 50, or 100, or 1000 cells in order to be doubled once.' The former of the above assumptions holds good exactly for the boundary of the cambial zone towards the wood; the second only applies to particular cases. In other cases, in which a successive increase of size of the secondary elements goes on, the relation is still less favourable to the multiplication of the radial rows. In fact, according to these considerations, the radial divisions in the initial layer must take place rarely in comparison to the tangential ones, and indeed the former are found to appear here and there in individual cells, in the course of successive secondary growth, without any demonstrable order of succession.

In the *medullary rays* the course of the secondary growth and of the divisions is in general essentially similar, yet at least in the most frequent case, to be described below, of radially elongated, parenchymatous elements of the medullary ray, it may be simpler as regards the divisions, the cells following the growth of the wood-strands for a longer time by radial extension, and the divisions happening more rarely than in the strands; they produce on the one side a new initial-cell, and on the other a new tissue-cell directly, and without any further previous divisions.

In addition to the divisions by *vertical longitudinal walls*, which alone have hitherto been regarded, *transverse divisions* occur in the formation of the secondary parenchyma, and no doubt oblique ones also in the origination of small medullary rays. These can only be discussed below, after describing the conditions of form of the cambial cells.

If we wish to designate by the name *cambium* a zone strictly distinguished from wood and bast, it consists, in accordance with what has already been said, of two, or rather of three, different layers of cells, namely (1) the single *initial layer*, and (2) the *tissue mother-cells*, including (*a*) those of the wood-side, and (*b*) those of the bast-side. The contingent modifications in the case of the medullary rays need not be repeated here. On the two layers of mother-cells border the products of their division, which already belong to the wood or to the bast. As the definitive formation of these requires some time, and they must at their first origin be similar to their mother-cells, a sharp distinction between them and the cambial zone is usually very difficult in practice, even in the condition of winter's rest; in descriptions they are therefore usually comprehended under the term cambium. We may distinguish them from the true cambium as *young wood* or *young bast*; in cases, however, where this distinction is not practicable, or is a matter of indifference, while on the other hand a distinction is required between the mature wood and bast and the collection of zones just described, the latter may be included under the general name of *the zone of young secondary growth*, or the *young secondary growth*, the term *young* secondary growth being understood as opposed to the developed secondary growth, consisting of wood and bast.

The *structure* of the cambium, and of the young wood and bast, has been given above, as regards the arrangement of the cells when seen in cross-section.

In each portion of the cambial zone, the form of the cells is identical with or similar to the general form of the elements of that section of the mature wood and bast which borders on it in the radial direction. (Figs. 198, 199.) Parenchymatous medullary rays are bordered by portions of the cambium, in which the shape of the cells is almost identical with that in the rays themselves, except that the relative radial diameter is on the whole smaller; while the bundles of wood, and the rare medullary rays composed of fibrous cells, are bordered by cambial cells having the form of elongated fibrous elements. Regarded more minutely, the form of these elongated cambial cells is very uniform in all the known cases. It was first accurately recognised by A. Braun[1], though only indicated by him, and has lately been fully described by Velten[2]. It is that of a rectangular prism, of which the radial transverse diameter is smaller than the tangential (on the average about half as long), while the ends of it, owing to an inclination of the radial lateral walls to the radial plane, form a sharp edge, lying radially and almost horizontally. The inclination of the lateral walls is usually confined to one side, and then directed alternately to the right and left, more rarely (e. g. Caragana arborescens, Cytisus Laburnum) the two radial surfaces are inclined to one another like a roof. The steepness of the inclination varies, partly according to the individual case, partly, in its average degree, according to species; and is on the whole the greater, the more the cells are elongated; the relatively short cambial cells of Tilia parvifolia, for example, have their end-surfaces inclined at about 45°, the relatively very long ones of Hamamelis virginiana are quite gradually tapered and pointed, as seen in the tangential view. Very slightly inclined or horizontal terminal surfaces only occur in isolated cases, especially above, or at the side of medullary rays. (Fig. 199.) From the conditions of form described, it follows that the elongated cambial cells, which, as meristem, are in uninterrupted contact, also form, as a rule, uninterrupted longitudinal rows, and only form alternating horizontal rows in the case of uniform inclination of the two radial surfaces.

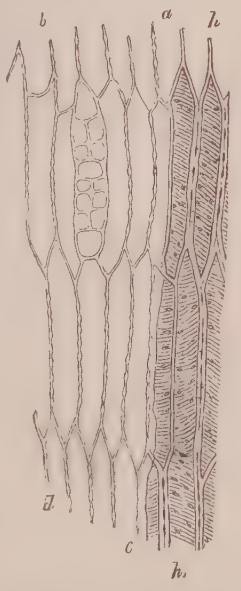

FIG. 198 — Cytisus Laburnum three-year-old branch, during the winter's rest (March); tangential section (145). *a c b d* the zone of secondary growth and cambium, containing a medullary ray above, and bordering on the autumn wood, *h*, of the previous year.

The absolute average size of the cambial cells varies according to the species, as will be stated below (Sect. 153). In certain cases it remains on the average the same during the whole growth in thickness, or increases continuously for a series of years, until a size is attained which remains approximately constant. And in fact this

[1] Monatsber. d. Berliner Acad. 7 Aug. 1854, p. 50 d. Sep. Abdr. Anmerkg.

[2] Botan. Zeitg. 1875, p. 811.—Compare also Sanio, Botan. Zeitg. 1863, p. 108.—N. Müller, Bot. Unters. Heft IV.

increase extends to all the diameters, so that the general form remains, if not exactly, yet approximately, the same.

The *structure* of the cambial cells is given in its most important points, by the

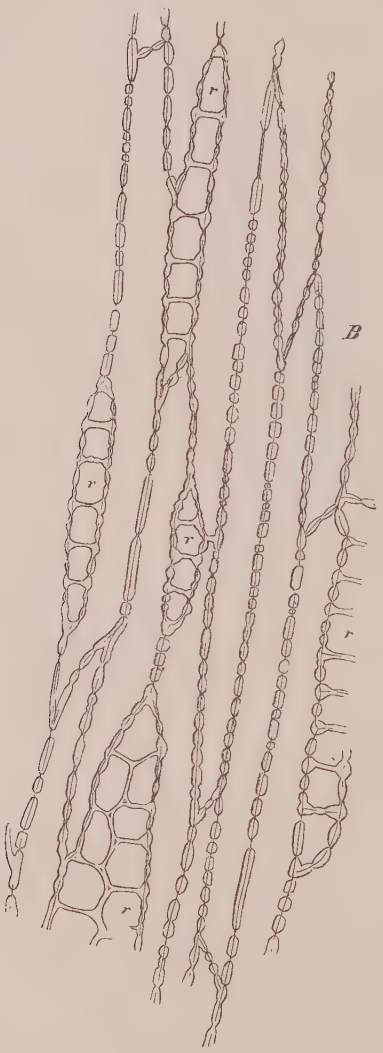

Fig. 199.

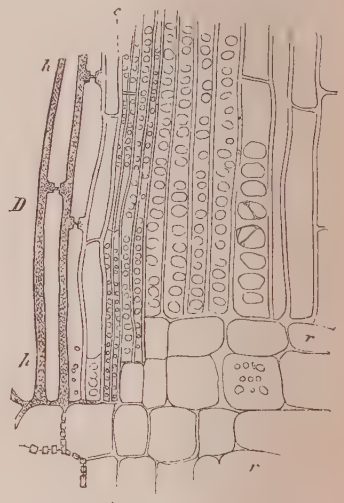

Fig. 200.

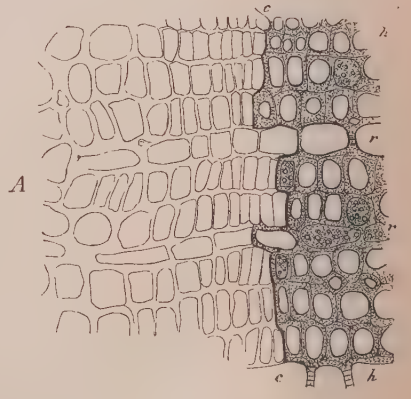

Fig. 201.

FIGS. 199—201.—Fraxinus excelsior. Internode of the stem, two years old, during the winter's rest, beginning of March (375). Fig. 199. Tangential longitudinal section through the layer of the zone of young secondary growth, bordering directly on the mature wood; *r* medullary rays.—Fig 200. Radial longitudinal section. *D*, *h* mature wood; *c*, *c'* limiting layer between this and the young secondary growth; the latter has rows of round pits (shown with too dark an outline) on the radial lateral walls, and passes over on the right into the inner zones of the bast; *r* medullary ray.—Fig. 201. Transverse section. *c c*, *h h* mature wood of the previous year, shaded; *c—c* limit between this and the young secondary growth succeed ng it on the left; *A* bast; *r* medullary rays.

statement of their meristematic properties. They are furnished with densely granular protoplasm, and with a well-defined nucleus, which is spindle-shaped, and in the elongated

cells is elongated in the same direction as they are; in the medullary rays of many woody plants (Vitis, Begonia) they contain chlorophyll, and in winter small starch-grains (Vitis, Aristolochia Sipho, &c.). Their cellulose walls are thin and delicate at the time of active growth, yet even here the difference between the radial and tangential surfaces, to be mentioned immediately, frequently and perhaps always appears, or is at least indicated. At the commencement of the winter's rest, the tangential walls of the elongated cells remain smooth and relatively thin; the radial walls, on the other hand, become considerably thickened, the highly refractive thickening mass being interrupted by a single longitudinal row of roundish pits. In the medullary rays a similar thickening takes place, and on their limiting surfaces towards the elongated cells there is a formation of pits corresponding to that on the latter (Figs. 198, 199–201). On the recommencement of the period of growth, the thickening mass appears to be again dissolved, at least in part.

These peculiarities of structure are shared by the cells of the young wood and young bast, as well as by the cambium. These cells may also enter with the latter into the condition of winter's rest. If, during the latter period, the zone of young secondary growth between the mature wood and bast be investigated, concentrically and radially arranged layers of cells are found, with the radial walls thickened as described; on the one hand, they are sharply limited towards the youngest mature wood, which is distinguished by its thick lignified walls; on the other hand, towards the bast, though here the limitation is less sharp, at all the points where the mature elements have slightly thickened and non-lignified walls. The number of the concentric cambium-like layers varies, frequently even in immediately contiguous radial rows; a fact which finds its explanation in the want of uniformity in the course of the cell-divisions in the latter, as mentioned above. In the simplest case only the single initial layer lies between the mature elements of the wood and bast: in its perfect form I have observed this only in the case of Juniperus communis (comp. below, Fig. 207). Usually the cross-section shows 2-4, or even more concentric layers of apparently similar, tangentially flattened cells, and only very accurate investigation teaches that these are non-equivalent, one being always the initial layer, while the others are partly tissue-mother-cells, partly young wood or young bast. The latter fact often appears especially clearly on the side of the wood, when growth begins anew after the winter's rest, for then certain of the cells are found undergoing extension to form members of vessels, directly and without further divisions (e. g. Vitis vinifera). Thus, even during the winter's rest, the layers of the true cambium are not distinguished either among themselves, or from the young bast and young wood by any characteristic structure; on the contrary, the entire zone of secondary growth, whether consisting of all its possible parts, or of the cambium, or the initial layer alone, may enter upon the winter's rest, and then assumes everywhere the same structure.

Having finished the description of the zone of secondary growth, we still have to return to the transverse and oblique cell-divisions taking place in it, which were left unexplained above. In the medullary rays these do not occur, or, if they do, are irrelevant. In the elongated elements, on the other hand, they appear as a constant and essential phenomenon.

(*a*) In the tissue-mother-cells they appear universally where short parenchymatous cells which do not belong to the medullary rays, and septate fibrous cells, are

formed within the secondary wood and bast; wood-parenchyma, bast-parenchyma, &c. (Fig. 202.) The transverse divisions take place once or oftener, and accordingly the height of the products of division is unequal from the first; from the different insertion of the transverse walls on the lateral walls, and the relative thickness of the two in the mature tissue, it may be conjectured that the transverse divisions take place in the one case in the early condition of the tissue-mother-cells (wood and bast parenchyma), in the other case in cells already belonging to the young wood or young bast (septate fibrous cells); on this point, however, more exact investigations have not as yet been made. Comp. below, Sect. 144.

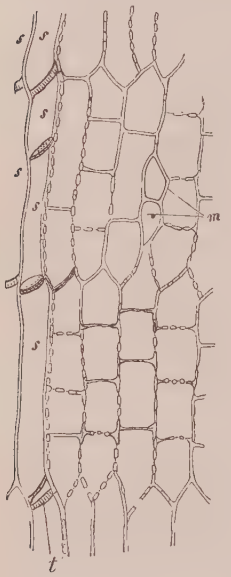

FIG. 202.—Cytisus Laburnum; tangential longitudinal section through the innermost layer of bast of the same branch as Fig. 198; magnified as in the latter. *s* members of sieve-tubes; *t* a sieve-plate lying deeper than the surface of section; *m* small medullary ray, two cells high. The remaining elements are parenchymatous cells of the bast, the origin of which by transverse division of the cambial cells becomes clear on comparison with Fig. 198.

Transverse divisions of the tissue mother-cells, or of the young wood-cells, are found in some instances before the formation of vessels with short members. The members of wide vessels with horizontal limiting surfaces may be shorter than the cambial cells from which they arise; the difference in length may, however, be due to the fact that, as they become wider, their height is diminished by displacement of the oblique terminal surfaces into the horizontal position[1]. In other cases however, e. g. in that of Vitis observed by Cohn[2], and in that of Acacia longifolia observed by Sanio[3], the shortening of the members of the vessel is so considerable that it does not find a sufficient explanation in this displacement, but rather necessitates the supposition of a transverse division.

(*b*) In the initial layer those transverse and oblique divisions of the elongated cells have to take place, by means of which new small medullary rays, consisting of short parenchymatous cells, originate within the bundles of the wood. This follows almost with certainty from the fact that the medullary ray, from its first appearance onwards, extends through the initial layer, towards wood and bast. The only other possible supposition would be that its first origination is due to divisions which extend, in the same direction, through cambium, young wood, and young bast. The first formation of a small medullary ray from elongated cambial cells is hard to observe, and is at present not very clearly known[4]. From the position of very small medullary rays, only one cell in breadth, and one or a few cells in height, as seen in tangential sections through the cambium and the zone of secondary growth, it may be stated that they originate either by single or repeated transverse division of an end of an elongated cambial cell, or by the cutting off of a portion of the radial lateral wall of the latter, by means of a (mussel-shaped) wall of division, with its concave side turned towards the

[1] Sanio, Botan. Zeitg. 1863, p. 122.
[2] Bericht über d. Verhandl. d. Schles. Gesellsch, Bot. Section, 1857, p. 44.
[3] Pringsheim's Jahrb. IX. p. 56.
[4] See N. Müller, Bot. Untersuchungen, IV. p. 181.—Velten, Botan. Zeitg. 1875, p. 842.

radial wall in question. (Comp. Fig. 202 *m*.) In the first cell thus formed, further transverse divisions may then ensue. In the frequent case where a medullary ray, originating as described, increases in height in the successive zones of secondary growth, both as regards its absolute size and the number of its cells, the various possible modes in which new cells may be added may easily be perceived, but the actual process has not been established with certainty. Further, it is not clear whether a small medullary ray may not be formed by repeated transverse division of an entire elongated cambial cell, or even of several one above another.

Sect. 137. As follows from their mode of development, the secondary elements of the wood and bast are always at first arranged in radial rows, if we except many groups of sieve-tubes. A growth in thickness of the masses of tissue lying inside the actual zone of secondary growth, such as would result in a displacement of the radial rows, takes place in the case of the wood exclusively during the development of the innermost layers, which are affected by it in the way of displacement or tangential extension; at a later period nothing of the kind occurs; in the case of the bast the conditions are no doubt different, owing to the continual widening of the zone of secondary growth, but the displacements following from this, which are to be described below, affect only the old external zones to any considerable degree.

The secondary elements must therefore maintain their original radial arrangement:

(1) When the form and length which they had in the cambial stage undergoes little or no change on their definitive development.

(2) When, although they become larger than the cambial cells, they maintain a form similar to the latter, and when, in particular, they have terminal surfaces inclined only towards the radial plane, where they abut on and penetrate between one another.

The first case occurs almost without exception in the medullary rays of normal structure (for the exceptions in the case of Atragene, Casuarina, &c. see below), in most parenchymatous masses of the wood, and in short tracheides, e.g. those of Cytisus Laburnum, &c. It is true that the height and breadth here frequently increase somewhat, even in the medullary rays[1], on the transition from the cambium to the definitive condition, but only in a slight degree, which does not alter the general grouping.

The second case applies to the elongated elements (fibrous cells, woody fibres, tracheides) of the wood of many, and the bast of most plants which form wood. Even, however, in cases belonging to this category, the longitudinal growth of the parts passing out of the cambial condition is trifling, as will be shown in the following paragraphs.

The conditions in question are present, almost without exception, in all parts of the wood and bast of the Coniferæ; in the Dicotyledons they are tolerably general in the soft bast, with the exception, however, of those cases which are characterised by irregular groups of sieve-tubes.

The sclerenchymatous fibres of the bast maintain their radial arrangement, for example, in Carpinus, Corylus, Ostrya, Liriodendron, and Magnolia acuminata and

[1] Compare Hofmeister, Pflanzenzelle, p. 164.

tripetala[1]. The above-mentioned elongated elements of the Dicotyledonous wood preserve their radial arrangement, for example[2], in Cunonia capensis, Viburnum Opulus, Staphylea, Hamamelis, Nerium, many Asclepiadeæ, Rhus typhinum, Jatropha Manihot, Laurus nobilis, Camphora, Aesculus, Verbena maritima, Broussonetia, Catalpa, Paulownia, Hydrangea hortensis, Justicia carnea, Fuchsia, Melastomaceæ[3], &c., which are chiefly, though not exclusively, plants with leaves in whorls; not but what with similar phyllotaxis a different arrangement of the elements may occur, as will be shown by facts to be mentioned immediately.

The original radial arrangement is, on the other hand, disturbed or obliterated:

(1) In groups of elongated elements, which show a great elongation on transition from the cambial condition to that of mature tissue, in the course of which they insert their tapering ends, which are the principal seat of growth, between each other, and acquire terminal surfaces which are inclined not only towards the radial rows, but also in other directions, or even show curvature and torsion of their ends.

(2) When certain of the originally similar elements undergo considerable growth in the transverse directions, on attaining their definitive development.

The first case perhaps occurs during the formation of many irregular groups of sieve-tubes, but this has not been minutely investigated, and is doubtful. It certainly takes place, however, in the case of those fibrous elements, which in the mature condition do not show any regular serial arrangement, and which often grow to many times their original cambial length: as in the groups of sclerenchymatous fibres in the bast of many Dicotyledons, e.g. Tilia (Fig. 211), in the fibrous cells, fibres, and elongated tracheides in the wood of Leguminosæ (Cytisus Laburnum, Caragana, &c.; most beautifully, on account of the contrast with the other elements of the wood, which maintain the cambial form and length, in Herminiera Elaphroxylon, comp. Sect. 150), Ulmus suberosa, Morus alba, Celtis australis, Tamarix gallica, Ilex aquifolium, Cornus sanguinea, Pyrus, &c.

The second case occurs universally in the development of wide vessels. Originally similar to the other elements, the members of the vessel often become expanded to many times their initial size; the neighbouring elements thus become not only displaced, but often transversely deformed in the direction of the surface of the vessel, compressed, or even completely crushed, so that mere rudiments remain[4]. According to the degree of expansion, and the number of the wide vessels in any portion of the transverse section, the general arrangement of the elements is influenced by them.

It need scarcely be mentioned that all the phenomena described may occur in various degrees, so that cases intermediate between the extremes may exist.

Sect. 138. The collective zones of secondary growth, cambium, young and mature wood, bast, &c., which have hitherto been regarded with immediate reference to a single transverse section of stem and root, if *traced longitudinally*, are continued, as uninterrupted layers, both through the successive portions of the same axis, and

[1] Hartig, Forstl. Culturpfl. p. 256.—Sanio, Botan. Zeitg. 1863, p. 107.
[2] Compare Sanio, *l.c.* pp. 107, 115.
[3] Vöchting, *l.c.*
[4] For a minute description, see Velten, Botan. Zeitg. 1875, p. 809, &c.

from the main axis into the lateral shoots; and in fact each of the distinct layers of any transverse portion is continuous with the equivalent and simultaneously formed layer of the successive succeeding portions; the cambial layer of a shoot formed in one year, or its yearly production of wood being continuous with the like layers in the next year's shoot, &c.

The *longitudinal course of the single elements*, especially of those which are elongated, as appearing in the direction of the 'long grain' of the wood and bast, presents a series of remarkable phenomena, which, in a certain though not strict sense, are independent of those hitherto discussed. In treating of them we will here leave out of consideration the *torsion* of the entire masses of wood and bast in twining stems, in so far as this is in immediate relation to the torsion of the whole twining part, as the description of the latter phenomenon forms no part of the present work [1].

In stems with a straight and vertical growth, the elements in question usually have their longitudinal axis in an oblique position, deviating from the vertical, and this is the case both in bast and wood, the latter having been the subject of more exact investigations, which are here to be principally regarded [2].

The deviation from the vertical is usually less conspicuous in the direction of the radial plane; although it must take place in this direction in the case of the above-mentioned bundles with elements penetrating irregularly between each other, e. g. in the wood of Fraxinus and Cytisus Laburnum. It is clearly seen, even on observation with the naked eye, in the case of the Guaiacum wood, in which the fibres of successive concentric layers have their ends passing between each other obliquely in the radial direction (though to a less degree than in the tangential direction).

In many woods the oblique position in the tangential plane appears more clearly. As a rule its direction is the same for all the elements of each concentric layer, and on observation of the surface is indicated by an oblique 'grain' or striation running round the whole stem. The angle at which the striæ cut the vertical varies, partly according to the species, partly in individual cases. According to Braun it reaches its maximum—as much as 45°—in Punica Granatum; then follow Sorbus Aucuparia (up to 40°), Syringa vulgaris (up to 30°), Æsculus Hippocastanum (10°–20°); smaller values are more frequent, e. g. usually 4°–5°, rarely as much as 10° in Pinus sylvestris, 3°–4° in Populus pyramidalis, Betula alba, &c. 'In many cases,' says Braun, 'especially in Pinus, I have convinced myself that specimens with shorter internodes usually show greater degrees of torsion, than those with longer ones.' The inclination is also said to alter with the age of the tree, becoming greater in the later secondary layers in Punica, and smaller in Pinus.

The direction of the inclination has been found to be invariably the same in the case of many trees; right-handed (in the sense of Mechanics) in Æsculus Hippocastanum, left-handed in Populus pyramidalis. Other trees show one direction as the rule, the other as the exception, e. g. Pyrus communis, Carpinus, chiefly right-

[1] On this subject reference may be made to H. de Vries, in Arbeiten des Botan. Instituts zu Würzburg, Heft III, and the earlier literature on the subject which is there cited.

[2] See A. Braun, Ueber den schiefen Verlauf der Holzfaser, Monatsber. d. Berliner Acad. 7 August, 1854; Botan. Zeitg. 1869, p. 747; 1870, p. 158.

handed Salix alba chiefly left-handed. Further, it either remains the same in the successive secondary layers of the same stem, or, in many kinds of trees, as Pines and Firs, the direction changes, becoming reversed after a number of similarly inclined layers.

Among 167 species of Dicotyledonous woody plants and Coniferæ, to which Braun's investigations extend, the oblique grain is present in 111; in the rest, e. g. Pinus Cembra, Populus monilifera, Ulmus campestris and effusa, Fraxinus excelsior, Clematis Vitalba, it has not been observed.

The arrangement of the fibres in the Guaiacum wood is different from their uniform obliquity round the entire stem in the trees hitherto mentioned. Here the grain curves backwards and forwards with short undulations, in each layer of wood, often cutting the vertical at 45°, assuming different directions in successive narrow layers, not in the broad (annual?) rings. This arrangement, showing a different direction in every small subdivision of the wood, and the interlacing of the elements, in addition to the radially oblique position and interweaving above mentioned, are the causes of the impossibility of splitting the Guaiacum wood in the radial, and the difficulty of doing so in the tangential direction.

The facts mentioned, and especially the reversal of direction, in successive layers of wood, are sufficient to show, what all accurate investigation confirms, that the oblique grain is a purely anatomical phenomenon, independent of the external conformation of the plant. It is also only perceptible externally in the case of injuries which lead to the splitting of the tree in the direction of the grain, such as frost cracks, splitting of the cortex in the direction of the grain of the bast, e. g. in Tilia, Syringa, Juniperus, and Thuja, or in the case of an excessive local swelling of the layers of wood, starting from branches or roots, as in many trees (Punica, Carpinus, Populus pyramidalis); this leads to the formation of ridges, which run round the stem obliquely, in the direction of the grain.

A plausible anatomical explanation of the oblique position of the elongated elements of the wood is afforded in a general way by their conditions of length. As will be shown below, the elongated elements in a number of woody plants increase successively in length for a series of years. As the total length of any portion of the stem remains unchanged during the secondary growth in thickness, and as, further, no enlargement of individual cells at the cost of others which become obliterated occurs, either in the cambium or its products (with the exception of the relatively inconsiderable phenomena connected with the expansion of vessels mentioned above), but on the contrary, all the cells of any layer parallel to the periphery grow, and become larger, or at any rate not smaller, it follows that the progressive increase in length of the elongated elements must result in their position becoming oblique; in the one case this affects the cambial cells themselves, in the other the fibrous elements in process of differentiation. It may at once be added that in the case of stems with the fibres in a tangentially vertical position, as, for example, Fraxinus, the length of those belonging to successive layers must remain the same, or any difference in length must be equalised by radial obliquity only, a point which has still to be investigated. These considerations render the phenomenon intelligible it its main outlines, but by no means explain all the details. It is open to question whether the above-mentioned differences in length are sufficient by themselves to

explain the extent of the angle of inclination; the similar direction of the inclination in the individual layers, its reversal, and more especially its alleged diminution in the later layers in Pinus, &c., all remain to be explained. The basis of such an explanation is to be sought in a more complete determination of the size and form of the organs in question, than has yet been made.

The undulated course of the woody fibres, which appears on cicatrised wounds, &c., and gives the character to knotted and gnarled wood, may here be excluded from minute consideration, as it is a pathological phenomenon[1].

Sect. 139. Plants with typical Dicotyledonous structure of the stem, as well as the majority of those Dicotyledons and Gymnosperms which are anomalous in this respect, form, with very rare exceptions, a cambial ring in *the root*[2] at an early period, and this, when once present, shows a completely similar growth and new production to that in the stem, although in each particular case definite special differences exist between stem and root, which are to be discussed below.

The first origin and orientation of the cambial ring must, on the other hand, be different from that in the stem, in consequence of the different original general structure in the root. It originates in the axial vascular bundle. The process begins with growth in thickness and tangential division of that layer of cells which borders on the inner surface of the phloem-groups, and in fact it proceeds from the middle of each of these groups towards its two lateral margins, and thus also towards the outer corners of the xylem-plates. The products of the tangential division are cambium and young secondary thickening. In the usual case of abundant growth in thickness, the tangential divisions eventually reach the pericambial cells lying outside the xylem-plates, and are continued over the latter, thus uniting the originally separate portions of the cambium to form a closed ring. As follows from the original arrangement and form of the xylem- and phloem-groups in the root-bundle, the general transverse section of the cambial ring, at its origin and before its completion, is a figure following the outline of the xylem body; in the diarch bundles it is a narrow ellipse, in those with more than two rays it is a polygon, with as many blunt corners and concave sides as xylem-plates are present. As, however, the cambio-genetic production of tissue on the side of the wood takes place unequally all round, and is the more abundant the nearer it is to the original starting-points of the formation of cambium, the phloem-groups are rapidly shifted towards the outside, and the concavities of the ring become flattened, so that its transverse section soon assumes a permanent, approximately circular form.

It is only in the comparatively rare cases of slight growth in thickness that the concavities between the original xylem-plates are permanent, and that the union of the original portions of the ring round their angles fails to take place; the formation of cambium is in some few cases entirely wanting, comp. p. 355. In other cases the tangential division in the neighbourhood of the xylem-plates is conspicuously less than that opposite the original phloem-groups; the cells in the former position

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[1] Compare Schacht, Lehrbuch, p. 67.—Göppert, Nachträge zu d. Schrift über Inschriften, &c., u. über Maserbildung, Bresl. 1870.—Idem, über die Folgen äusserer Verletzungen der Bäume, Bresl. 1873.—Ratzeburg, Waldverderbniss, I.—Nördlinger, Forstbotanik, I. p. 274.

[2] See Van Tieghem, Ann. Sci. Nat. 5 sér. tom. XIII. p. 185, pl. 3, 4, 8.

follow the growth in thickness chiefly by means of radial extension, so that, as seen in transverse section, the small-celled ring appears interrupted at the xylem-plates by rows of larger cells, e. g. Cucurbita, Urtica (Figs. 203, 204).

The production of tissue by the cambial ring or its segments, when once originated, maintains the same course as that described in the case of the stem. Any special differences in the succession of the divisions are, at the present time at least, unknown. The mass of tissue given off internally is to be termed the wood, the peripheral mass, the bast. Both are divided into wood and bast bundles, which correspond to one another in the same way as in the stem, and may be comprehended under the name *strands*, and into radial bands composed of non-equivalent elements, which alternate with the strands, and in the root no doubt always consist of parenchyma; these are the *medullary rays*.

The original large medullary rays are obviously excluded in the case of the root. As regards the arrangement of those rays which are present, and the dis-

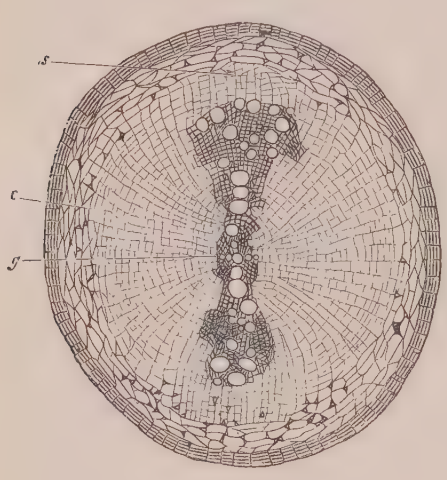

Fig. 203.

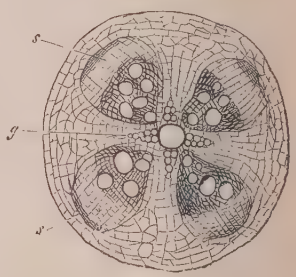

Fig. 204.

FIG. 203.—Urtica dioica; transverse section of a small subsidiary root from the rhizome (80). *g* original diarch xylem-plate; crossing it are two secondary bundles of wood, separated by broad bands of parenchyma (medullary rays); outside each, at *s*, is the bundle of bast belonging to it. Secondary cortex is present all round, with numerous scattered sclerenchymatous fibres, indicated as dark spots; the whole bounded externally by periderm. *c* layer of cambium or young secondary growth. The primary cortex has been cast off.

FIG. 204.—Cucurbita Pepo; transverse section of the main root of a young plant (40). *g* xylem body of the axial bundle, its four rays united in the middle by a large pitted vessel; four secondary bundles of wood alternate with them; *s* the original and secondary phloem-bundles. The primary cortex of the root has been replaced by periderm and cast off.

position of the strands which is determined by them, two main types are to be distinguished, though these are not sharply contrasted in all cases.

(1) A main medullary ray (usually very broad) appears opposite the angle of each original xylem-plate, the same number of main strands alternating with the main medullary rays, e. g. Centranthus, adventitious roots of Tropæolum, Urtica dioica (Fig. 203) among diarch roots; the main root of Cucurbita (Fig. 204), Phaseolus, Convolvulus tricolor, and many others among the tetrarch forms; adventitious roots of Cereus grandiflorus, Clusia, Cucurbita, and Artanthe among the polyarch root-bundles. Comp. van Tieghem, *l. c.*

(2) The whole periphery of the primary bundle acquires fascicular elements,

between which only small medullary rays exist, with an arrangement not corresponding to that of the primary xylem-plates. The entire secondary growth thus forms a cylindrical strand, without main medullary rays, e. g. Taraxacum, Scorzonera hispanica, Rubia, Thuja, Taxus, Cupressus, &c.

On the connection of the bundles of secondary wood with the primary plates, see Sect. 152.

For the further growth of the bundles and medullary rays when once formed, the successive subdivision of the former by new medullary rays, and the structure of the cambial layer, the same general rules hold good as in the stem.

The divisions in the cambial zone also appear to follow in general the same rules as in the latter, though this remains to be investigated. The frequent appearance of secondary intermediate strands in the broad medullary rays, especially of fleshy roots, is worthy of notice.

As a rule, the beginning of secondary growth takes place in the root immediately after the differentiation of the primary tissues; in the cases mentioned of feeble development on the other hand, as well as in the adventitious roots of Clusia, Cereus, and Piperaceæ, it begins relatively late, so that each portion of the root at first remains for some time in the primary condition.

II. The Wood.

1. *Distribution and form of the zones of secondary thickening.*

Sect. 140. In the native Dicotyledons and Conifers the wood acquires in every period of vegetation an increment of growth, the development of which begins in spring with the unfolding of the buds, and, with the exception of the roots of Dicotyledonous trees, reaches its end in autumn, starting afresh after a period of rest in winter; in the roots of native Dicotyledonous trees, on the other hand, it continues to make slow progress throughout the winter, and only reaches its end on the beginning of a new period of growth, whereupon it immediately begins again [1].

The product of each period of secondary growth, corresponding in our climate to an annual period, is, as a rule, distinguished from that of the earlier and later periods, by definite differences of structure in the limiting layers, which are to be described below. It is therefore called an annual zone, annual layer, or annual ring, and its limiting layers just mentioned are called *spring-wood* and *autumn-wood*.

The consideration of the zones of secondary thickening may conveniently start from those which are severed into distinct annual layers, especially as this is by far the most frequent case.

The form of the annual rings has been investigated in the case of trees and shrubs. It is well known, and does not require any detailed statement here, that their average breadth shows great variations in the same individual, according to age, and to the action of more or less favourable conditions of vegetation [2], and that under

[1] Von Mohl, Botan. Zeitg. 1862, p. 313.

[2] Compare the works of Nördlinger and R. Hartig, to be cited below.—Further, H. de Vries, Einfluss des Druckes auf d. Bau, &c. des Holzes, p. 96; Flora, 1872, p. 241, 1875.

similar, or equally favourable conditions, the average breadth varies considerably according to the species. Compare, for example, the broad rings of Paulownia and Ailanthus, with those of Citrus and Cornus; Pinus silvestris and Abies pectinata with Taxus, &c. In the stem of the young tree the breadth of the annual rings increases, under otherwise similar conditions, for a number of years, then remaining for a series of years at an average maximum, but decreasing again in advanced age. In the yearly shoots formed on the thickened stem the average maximal breadth of ring is attained in the first year, or in the first few years[1]. It is shown even by superficial observation, which may be easily confirmed by more minute research, that the yearly secondary growth in the lateral branches and roots of a tree is less than that in the stem.

The breadth of each ring is, in the regularly developed *stem*, uniform all round, though even in this case it may be unequal in consequence of unequal acceleration of the growth on different sides, the ring thus becoming undulating or eccentric, even to such an extent as to be wholly absent on the deficient side. The rings of one and the same cross-section of the stem often show the most various differences in all these respects, forming, as it were, records of the history of its growth and nutrition; in certain woody plants, to be mentioned below, such inequalities of growth are typical.

Unilaterally unequal development of the rings, and consequent eccentric thickening, are the rule for the *lateral branches* of the stem and of the *roots*; and in fact in the lateral branches of most Dicotyledonous woody plants, the *upper side* is the favoured one, e.g. Acer pseudoplatanus, Alnus, Carpinus, Cornus, Corylus, Cratægus, Cytisus Laburnum, Euonymus, Gleditschia triacanthos, Fagus, Tilia, Prunus spec., Robinia, &c.[2]; on the other hand, in the Coniferous woods, and according to Nördlinger in Castanea, the *under side* is favoured. In *small stems* also, which for a series of years have grown upright, and increased uniformly in thickness all round, but have then been permanently brought into the inclined position by the pressure of snow, Nördlinger found that the rings formed from the time when the stems became oblique, were eccentric, and that in the Pines, Firs, and Larches the under side, in Oaks and Beeches the upper side is favoured. In the lateral roots of trees at the places where they arise from the stem, the upper side which is continued into the latter is the one favoured; at a greater distance from the stem the under side usually has the advantage, according to Mohl's opinion[3], but this point has not been decided for certain. Centrically developed roots of trees are, however, not actually rare.

In the case of our forest trees a series of investigations have been instituted on the average amount of the annual secondary growth of the stem in its successive transverse sections from base to apex, which of course always determines the general form of the stem[4]. In some cases the successive *surfaces* of the transverse section

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[1] Nördlinger, Der Holzring, p. 14.

[2] Compare Nördlinger, Holzring, p. 20.—Hofmeister, Allgem. Morphologie, p. 604.

[3] Botan. Zeitg. 1862, p. 274.

[4] Von Mohl, Botan. Zeitg. 1869. p. 1.—Nördlinger, Der Holzring, Stuttg. 1872.—R. Hartig, in Dankelmann's Zeitschr. f. Forst- u. Jagdwesen, Bd. III; and Botan. Zeitg. 1870, p. 505.—We may refer to these works for the older, very defective literature, and for many details not strictly belonging to our present subject.

of the individual layers has been determined, giving the 'growth in mass;' while in others the (radial) *diameter*, the *breadth of ring* has been measured, on the successive dimensions of which the form of the stem depends. The growths in mass and breadth of ring in a layer do not necessarily correspond one with another, because the former may be greater in its lower portion, where its periphery is larger, though the breadth of ring is smaller, than in its upper portion where the ring is broader. The following rules may hold good as giving the consistent result of the published investigations, which extend to the Oak, Beech, Alder, Silver Fir (Abies pectinata, D. C.), Scotch Fir (Pinus sylvestris L.), Red Fir (Abies excelsa Poir.), Larch, Weymouth Pine (Pinus Strobus L.), &c.

(1) In the *shaft*, i. e. in the unbranched stem between the basal 'stock' and the crown, the annual growth in mass increases in the case of trees which *stand free*, from above *downwards*; according to Nördlinger the average diameter of the ring always increases simultaneously, while, according to R. Hartig, this may increase or decrease, or remain the same, which agrees with the results of the radial measurements made by Mohl on three trees grown in the open, which showed increase in the upward direction. In *closely planted* trees, the average breadth of the rings increases in the upward direction, according to Nördlinger, Mohl, and R. Hartig, while according to R. Hartig's statement, which has been reasonably disputed by Nördlinger, the growth in surface or mass remains throughout approximately the same. Trees, the crown of which has become *stunted* in consequence of their being closely planted, show a diminution of the secondary growth in this direction, namely, from above downwards, which may extend even to its complete absence in the lower portion.

(2) In the *crown* the growth increases in the downward direction, both in the stem and branches.

(3) In the basal *stock* a considerable increase in the secondary growth and the average breadth of ring takes place in the older stems, i. e. in the outer layers; this starts from the upper side of the insertions of the roots, and may extend upwards to a different height (0·3–3 metres and more), according to the particular case. At the points of insertion of vigorous lateral roots, the secondary growth is locally increased in such a manner that the well-known projections of the stock, separated by furrows, and in the case of tropical trees attaining huge dimensions, may arise in the course of a few years.

The 'forms of growth' mentioned under (1) are subject to change in the same individual, when successively planted free, and in contact with others. For each particular species of our forest trees one or the other form of growth is the rule, and this depends on whether they usually grow in close contiguity throughout life, either wild or in forest culture (e. g. Beech, Silver Fir, Red Fir), or whether in their later years they become free (e. g. Scotch Fir, Larch, Oak, Alder)[1].

The dependence of the general form of the stem, whether it be more conical or cylindrical, on the conditions mentioned is self-evident. In the same way it is clear, that in the stems of exotic plants which deviate from the cylindrico-conical form, as the spindle- or barrel-shaped stems of Bombaceæ[2], the progression of the

[1] Compare R. Hartig, Botan. Zeitg. 1870, p 513.

[2] See e. g. the figure of Bombax Munguba in Martius, Fl. Brasil. Tab. physiogn. X.

annual secondary growth from below upwards must be different from that in our trees, in so far as the form is dependent on the thickness of the layers of wood, and not on that of the cortical layers or masses of pith. How far the one or the other explanation is the right one has not been made out in all cases in these plants. The Mamillariæ, for example, cited by Mohl as examples of barrel-shaped stems, owe their form, not to the successive increase or decrease in thickness of the layers of wood, but to that of the cortical masses of parenchyma.

2. *The forms of Tissue of the secondary wood.*

Sect. 141. The *forms of tissue* of which the secondary wood is composed[1] belong chiefly to the categories of *cells* (comp. pp. 5, 115, 121), *tracheæ*, and *sclerenchymatous elements*, especially *sclerenchymatous fibres*. They sometimes have their characteristic anatomical peculiarities, and the division of labour which these indicate, rigorously developed and carried out; sometimes, however, the division of labour is arranged in such a manner that while an element has the essential peculiarities and functions of one of these forms of tissue, and must therefore be classified with it, it further shares in the characteristics of another form.

In the tough strong woods of trees and shrubs, which have been the chief subject of investigation, the latter holds good of the elements of *all* forms, in so far that they are—in various degrees—thick-walled and sclerotic; a phenomenon which is not characteristic of the secondary wood generally, but only of that of the 'woods' so called in ordinary phraseology. In the very hard secondary wood of Convolvulus Cneorum, for example, all the elements both of the bundles and of the medullary rays are in the highest degree sclerotic; in the soft, fleshy, chiefly parenchymatous wood of the stem of Carica, Cheirostemon, many succulent roots, &c., only certain individual elements have that character. In the stem of Clematis Vitalba, the parenchyma of the medullary rays takes part in the sclerosis, in that of Atragene it does not, and so on.

In many woods one or the other form of tissue may be absent, and its functions be undertaken by others, as will be shown by the examples to be mentioned below.

Sect. 142. The *tracheæ* of the secondary wood appear partly in the form of vessels, partly as tracheides[2].

Of the forms of *vessels*, as distinguished by the structure of their walls, the reticulately thickened are present exclusively or principally in succulent soft woods, as in the stem of the Papayaceæ, and in many fleshy roots (Sect. 159). Reticulated vessels with large meshes are further characteristic of the wood of the Crassulaceæ[3], even of the species with hard wood. Reticulated vessels occur, together with pitted ones, in the Caryophylleæ, and may often be found in herbaceous Dicotyledons, which have been comparatively little investigated. The wood of the Mamillariæ and of species of Echinocactus and Melocactus contains only spiral and annular tracheæ, and in fact both vessels and tracheides: some have feebler thickening fibres, the

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[1] Sanio, Ueber die im Winter Stärke führenden Zellen des Holzkörpers., Halle (Linnæa), 1858. —Id Botan. Zeitg. 1863, p. 85, &c. The latter also contains detailed citations of the older literature.

[2] Compare Chapter IV.

[3] Compare Regnault, Ann. Sci. Nat. 4 sér. tom. XIV. p. 87.

transverse section of which is almost isodiametric, while those of others are ridge-shaped and deeply projecting as described at p. 156. The former are chiefly vessels, the latter usually tracheides; but the separation of the two forms is hard to carry out with certainty on account of the difficulty of establishing the presence or absence of the vascular perforations. The species of Opuntia and Cereus have reticulated vessels, which may be accompanied by tracheæ with the ridge-shaped thickenings above mentioned.

The cases described, however, constitute exceptions as compared with the great majority especially of arborescent or shrubby Dicotyledons. In the latter the vessels of the secondary wood are pitted vessels, the wall, apart from the pits, being either smooth, or with a fine spiral fibre on the inner side (comp. Fig. 205). The pits of the vessels are bordered and correspond one with another, at least on those surfaces which border on vessels or tracheides (comp. Sect. 38). On the surfaces bordering on non-equivalent elements, various conditions occur, which will be stated below, chiefly according to Sanio.

Where pitted vessels are adjacent to sclerenchymatous fibres with unbordered pits (comp. Sect. 143), the pitting may be wholly absent (Olea europæa, Fuchsia globosa according to Sanio); in most cases pits are present, though they are always less numerous than those on the surfaces contiguous with tracheæ, and they also differ from the latter in form. On the surfaces adjoining fibres with unbordered pits, the pits on the wall of the vessel are bordered, but smaller than those on the boundaries of vessels, in Hedera Helix, Euonymus latifolius, europæus, and Syringa vulgaris; they are unbordered in Sambucus nigra, racemosa, Acer platanoides, Salix acutifolia, hippophæfolia, Populus pyramidalis, Æsculus Hippocastanum, Rhamnus Frangula, Aucuba japonica, Pittosporum Tobira. The surfaces adjacent to parenchyma and fibrous cells have sometimes bordered, sometimes unbordered pits, and sometimes both kinds. The first, for example, is the case in Quercus pedunculata, Diospyros virginiana, Juglans regia, Porlieria hygrometrica, Spartium scoparium, Caragana arborescens, Sophora japonica, Acacia Sophora, Morus alba, Daphne Mezereum, Ribes rubrum, *Syringa* vulgaris, Casuarina equisetifolia, Hibiscus Rosa sinensis, Pæonia Mutan, Ficus Sycomorus, Olea europæa, Nerium Oleander, Tamarix gallica, Punica Granatum, Justicia carnea; these pits are unbordered in Hedera Helix, Sambucus racemosa, nigra, Æsculus Hippocastanum, Rhamnus Frangula, *Syringa* Josikæa, Solanum Dulcamara, Populus pyramidalis, Salix hippophæfolia, acutifolia, Vitis vinifera, Magnolia tripetala, acuminata, Hydrangea hortensis;—both kinds occur in Bombax Ceiba, Ficus rubiginosa, Jatropha Manihot, Fuchsia globosa and Eugenia australis.

As a rule the pits bordering on cells are relatively large; they are rarely small and very numerous (Hydrangea hortensis); where two kinds occur the bordered often differ from the unbordered also in their superficial outline. The pits of the vessel always correspond with the unbordered ones of the non-equivalent elements, and in fact those of the latter are always of the same breadth as the border of the pits on the vessel.

As an exception we must mention the wall destitute of pits with which the vessels border on the fibrous cells in Punica Granatum.

Where the lateral walls of the members of a vessel have a spirally thickened inner layer in addition to the pits, the spirals are always present on the surfaces adjacent to tracheæ, with one exception to be mentioned at the end; in certain cases they also exist on the surfaces adjacent to all the other, non-equivalent elements (Tilia parviflora, Pittosporum Tobira, Prunus domestica, Laurocerasus). In other cases the spirals are absent on the surfaces which border on parenchyma, while they are present on the others (Amygdalus communis and other Amygdaleæ); or they are absent where vessels border on one another and on parenchyma, and are only present on the surfaces which are adjacent to fibres.

The different forms of perforation of the transverse wall vary according to the particular cases (species).

The vessels are relatively thin-walled in most true woods, even in very hard woods, and are often remarkably delicate (Camellia japonica). More rarely the thickness of their walls is equal to that of the thickest-walled of the elements which accompany them, e. g. Fraxinus excelsior, Ornus, Nerium Oleander, Piperaceæ, Convolvulus Cneorum.

The *Tracheides* (Fig. 205) either constitute the only tracheal elements of the wood (Coniferæ, Wintereæ), or they occur together with other tracheal organs, especially vessels. They are characterised as tracheides by the properties indicated in Chap. IV. The structure of their wall is in the case of the Coniferæ and Wintereæ that of pitted vessels with bordered pits; in most Taxineæ there are also spirals on the inner side of the wall. In the second case the same holds good, with the addition that they then resemble the members of the narrower vessels of the same wood, either in all points, except the vascular perforation, or at least in possessing similar bordered pits to those of the vessels belonging to the same wood. As regards the spirally or annularly thickened inner layer, they usually agree with the vessels accompanying them, but not always: in Pyrus communis, Sorbus Aucuparia, and Staphylea pinnata the vessels have spirals, the tracheides not, in Philadelphus coronarius the converse is the case. In particular tracheides of many plants, we find, as an exception, isolated thickenings of the wall, projecting inwards in the form of blunt cylindrical pegs, or of bars running transversely from one side to the other. Both forms were observed by Sanio in Hippophæ rhamnoides, the latter in Pinus silvestris[1], and casually by me also in Drimys Winteri. The transverse bars lie in the radial direction, at least in Pinus and Wintera, and are continued as a single bar through many elements of a radial row. Peculiar transverse lines, which Sanio found on macerated tracheides of Casuarina (*l. c.* p. 117), still require explanation.

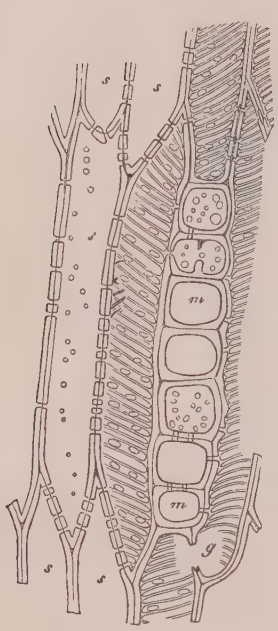

FIG. 205.—Cytisus Laburnum; tangential section through the same autumn wood as Fig. 198, p. 465. *s* intermediate cells, *m—m* medullary ray; in the second cell from the top is a peg-shaped thickening of the wall. The medullary ray is bounded on the left by an unperforated tracheide, on the right by a narrow vessel; at *g* is the perforation of the transverse wall of the latter. The lower longitudinal wall of the tracheide to the left was preserved in the preparation; the upper one, all but a very small piece, was removed in cutting the section; in the other tracheides and vessels the longitudinal wall facing upwards is drawn, the spiral fibres being shown in reversed direction, and the really bordered pits with only a single outline.

Where tracheides occur together with vessels or sclerenchymatous fibres, or both, two extreme cases may be distinguished as regards their form, namely, on the one hand, those which on the whole resemble the members of the smaller vessels in length and width, and abut on one another with a relatively slight inclination of their terminal surfaces; on the other hand, more elongated, 'fibre-like' forms, with long acuminate ends, sometimes even forked (Hippophæ, Casuarina torulosa, Staphylea pinnata), which penetrate between one another and between the non-equivalent elements.

[1] Compare above, p. 164.

The average length, expressed in hundredths of a millimetre, is, for example, according to Sanio's determination, in

	Tracheides most similar to vessels.	*Fibriform Tracheides.*
Fagus silvatica	39	75
Cunonia capensis	69	97
Casuarina torulosa	45	104
„ equisetifolia	48	75
Hamamelis virginica	70	80
Sheperdia canadensis	19	45

The first category includes those tracheides which also approach the vessels most nearly in the structure of the wall, while those belonging to the second are in this respect also less similar to the vessels, and approach the fibres in every point. If we survey the entire series of the woods investigated, there is on both sides, as well as between the two principal cases just distinguished, a continuous transition between the extremes [1].

The average thickness of the walls and the nature of the thickening layers [2] generally vary in accordance with the other differences and similarities, if the exceptional cases of very thick-walled vessels already mentioned be left out of account. The peculiar tubes, containing air, which form the floating apparatus of many Leguminous woods (Herminiera, &c.) must here be mentioned by way of supplement. In order to avoid repetitions, the description of them follows below, in Sect. 150.

Sect. 143. The *sclerenchymatous fibres of the wood*, shortly termed *woody fibres* (Fig. 206), are generally distinguished from those elongated tracheides which are more or less similar to them in form, by the structure of their wall. The latter is always destitute of the spirally-thickened innermost layer—although the whole wall may be striated and capable of splitting in a spiral direction,—and its pits, which are invariably slit-shaped, and lie in a left-handed oblique direction, are always present in relatively small numbers, often very sparingly, and differ in details from those of the accompanying vessels. While in many cases they are bordered here also (Quercus, Daphne, Liriodendron, Fraxinus, &c.), they are usually not bordered (Sambucus, Hedera, Clematis Vitalba, Syringa vulgaris, Ligustrum vulgare, Euonymus latifolius, Celastrus scandens), or so small that the presence of the border is difficult to determine. Both kinds of pits are mentioned by Sanio as occurring in Jatropha Manihot, those with a border being the more numerous. In this plant Sanio found two kinds of pits on the surfaces of junction between the fibres and the medullary rays, namely, small slit-shaped ones on the radial lateral surfaces of the cells of the medullary ray, but large round ones on their horizontal corners, towards which a small pit runs from each adjoining cell of the ray. In the other cases investigated, the pits of the fibres are of approximately equal size, on whatever form of tissue they may border.

The walls of the fibres are thickened, in a manner which accords generally with the fundamental rules holding good for all cell-walls; their usually comparatively thick middle layer [3] is as a rule homogeneous, at least without any conspicuously

[1] Compare Sanio, *l. c.* pp. 117, 118. [2] See Hofmeister, Pflanzenzelle. p. 196.
[3] Hofmeister, *l. c.*

apparent finer stratification and striation[1]; its thickness, however, is very unequal in different species and individuals. The walls are as a rule lignified. A not uncommon exception, however, occurs, inasmuch as one of the layers is of a manifestly soft, cartilaginous, gelatinous consistency, and is then excluded from the process of lignification, becoming violet immediately on treatment with preparations of iodine. This gelatinous layer (comp. p. 133) is as a rule the innermost one; it surrounds the lumen immediately, either as a narrow border (Jatropha Manihot, Morus alba), or usually as a thick, apparently swollen mass, filling the greater part of the lumen. In rare cases a layer enclosed between the lignified ones shows the characteristics in question; these often extend to the whole of the wall lying inside the outermost limiting layer ('primary membrane'). Lastly, the gelatinous layer may often be distinguished by its refraction, even when it is stained like a lignified membrane by preparations of iodine[2].

The occurrence of the gelatinous layer is strikingly irregular. Sanio found it especially among Leguminosæ (Cytisus Laburnum, Sarothamnus, Sophora japonica, Caragana arborescens, Gleditschia triacanthos), where it is of quite usual occurrence; also in Ulmus suberosa, Celtis australis, Hakea suaveolens, Morus alba, Broussonetia, Ailantus, Fuchsia globosa, Eugenia australis, Castanea, Diospyros virginiana, Corylus Avellana, Ostrya virginica, Populus pyramidalis, Betula alba, Alnus glutinosa, Enckea media, Eucalyptus cordata, Calycanthus floridus, Amygdalus communis, Prunus Laurocerasus, Jatropha Manihot, and Ficus Sycomorus, and he supposes that it occurs much more generally. It is, however, by no means generally characteristic of all the fibres of these woods, as it may be present or absent in different parts even of the same annual ring; while its occurrence is often rare, and even so isolated (Betula, Alnus) that one may repeatedly investigate a wood without finding it. Nor is its presence or absence connected with any definite special form of structure in other respects, or with the average thickness of the wall. It cannot therefore be regarded as a characteristic peculiarity of the fibres, the less so, as in particular cases (Hamamelis, Fagus silvatica, Casuarina) it also occurs in elements which, according to their other properties, belong to the class of tracheides which resemble vessels.

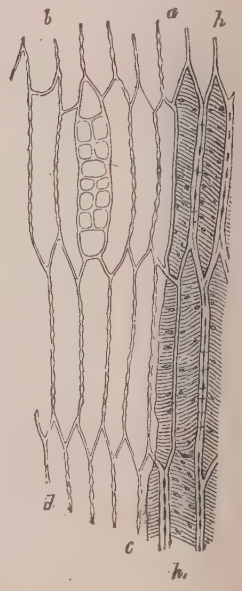

Fig. 206. Fig. 207.

FIG. 206. — Cytisus Laburnum; three-year-old branch during the winter's rest (March). Tangential section (145). *a b c d* the zone of secondary growth and cambium bordering on the autumn wood, *h* of the previous year, and containing a medullary ray above.

FIG. 207. — Cytisus Laburnum. Outlines of a selected short woody fibre, from the youngest annual ring of the same branch as that from which Fig. 206 is taken (145).

What was stated above in the case of the tracheides most closely resembling fibres, applies generally to the fibres themselves as regards form and size. Sanio (*l. c.* 106) adduces many examples of the occasional bifurcation of their acute ends. On the average their length exceeds that of the neighbouring tracheides the more, the more the latter

[1] Compare Sanio, *l. c.* p. 105.

[2] For details see Sanio, *l. c.* p. 103.

resemble vessels, comp. Figs. 206 and 207; in extreme cases it may be approximately equal to that of the tracheides (Syringa), or even somewhat less (Ribes).

The following mean values, as determined by Sanio in hundredths of a millimetre, may serve to demonstrate the relations of length :—

	Tracheides.	*Fibres.*
Sophora japonica	16	95
Sarothamnus scoparius	17	56
Ulex europæus	16	103
Celtis australis	26	87
Cordia pallida	27	111
Rhamnus cathartica	28	52
Æsculus Hippocastanum	26	43
Tilia parviflora	31	46
Salix acutifolia	33	53
Rhus typhina	32	35
Rhamnus Frangula	24	44
Quercus pedunculata	49	80
Prunus Laurocerasus	56	126
Populus pyramidalis	39	45
Hakea suaveolens	26	81
Eucalyptus cordata	34	60
Periploca græca	28	36
Daphne Mezereum	15	21
Spiræa chamædryfolia	33	35
Syringa vulgaris	50	51
Ribes rubrum	49	47

In the *contents of the woody fibres* shrivelled remains of protoplasm and of formed constituents of the contents can only be detected in rare cases where the wall is very thick and the lumen very narrow, as in the tough fibres of the wood of Viscum, and perhaps also of Leguminosæ, Quercus, &c. Further attention must, however, be directed to this point, which is difficult to make quite clear, on account of the scantiness of the remaining contents and the thickness of the wall. Even in the cases just mentioned air is certainly present, in addition to the remnants of the contents. In most woody fibres, however, the lumen contains nothing but air and water. It is manifest that they agree in this point with the tracheides, nor does it admit of doubt that in so far as this is the case they take part in the functions of the latter, and thus that we here have a case of the above-mentioned phenomena of incomplete division of labour. The sharp severance of the two organs cannot therefore be carried out without violence and uncertainty, especially as the characters assigned to them, and in particular the bordering of the pits, are on the one hand variable in different cases, and on the other are difficult to determine in practice, in the case of very small pits. It will therefore constantly be necessary to speak of tracheides resembling fibres, and of fibres resembling tracheides. On the other hand, however, many cases of sharp differentiation exist, as in the Leguminosæ mentioned, Quercus, and many others; these cases render the distinction necessary, and by taking these as the starting-point, it can be carried out even in the less clear cases.

Sect. 144. The *cells* of the secondary wood may be divided according to their form, into *fibrous cells*, and short *parenchymatous cells*.

1. The *fibrous cells* resemble the woody fibres more or less closely in form.

Like the latter they proceed from the longitudinal division of an elongated spindle-shaped tissue-mother-cell of the cambial zone, without any transverse divisions. In the thick-walled forms, a subdivision of the lumen into compartments may subsequently occur, by means of thin transverse walls, as is the case in the chambered sclerenchymatous fibres (p. 134): these are *septate fibrous cells*.

The elements in question, as follows from what has been stated, are products of the cambium, in which the cellular qualities persist permanently, or disappear slowly. In their further characteristics they are closely related to the other elements of the wood, namely, on the one hand, to the woody fibres, and on the other to the short-celled parenchyma. Of the two subordinate forms which result from these relations, the former may be termed *fibrous cells* in the strict sense, while the latter may bear the name of *intermediate cells*[1] (Ersatzfaserzellen) given by Sanio.

a. The former agree in their form, and in the structure of their walls, with the woody fibres, and thus certainly take part in the functions of the latter, into which they may gradually pass over completely. They are distinguished from them by the nature of their contents. The latter almost always contain starch (comp. p. 115): in Spiræa salicifolia Sanio found traces of chlorophyll; this appears more abundantly in the septate fibrous cells of the one-year-old wood of Vitis vinifera and Centradenia grandifolia. Tannin is contained in the fibrous cells of Vitis, and traces of it in that of Syringa vulgaris, while in the other woods investigated it is absent in these elements, even where it occurs in other cells.

In the wood of Punica Granatum, all the elements of which, with the exception of the vessels, are filled with starch[2], the grains contained in the fibrous cells are on the average considerably larger than those of the other cells.

Besides the plants already mentioned fibrous cells containing starch occur in the wood of Berberis vulgaris, Mahonia Aquifolium, Begonia muricata, angularis, Sambucus nigra, racemosa, Cheiranthus Cheiri, Salix cinerea (root), Ligustrum vulgare, Syringa vulgaris, Clematis Vitalba, species of Acer, Vitis vinifera, Celastrus scandens, Euonymus europæus, latifolius, Hedera Helix, Acacia floribunda, Robinia pseudacacia, Ficus elastica, rubiginosa, Sycomorus, Rhus Toxicodendron, Tamarix gallica; fibrous cells with slightly granular contents occur in Ephedra.

Septate fibrous cells occur in Coleus Macraei, Hydrangea hortensis, Fuchsia globosa, Aucuba japonica, Celastrus scandens, Euonymus latifolius, europæus, Spiræa salicifolia, chamædryfolia, Ceratonia, Hedera Helix, Pittosporum Tobira, Eugenia australis, Rubus idæus, Justicia carnea, Ficus Sycomorus, rubiginosa, elastica, Bignonia capreolata, Tectona grandis, Rhus Cotinus and Toxicodendron, besides the plants already mentioned; either the non-septate predominate (e. g. Spiræa salicifolia), or the septate, e. g. Vitis, Hedera, and Punica. Starch has always been found in the septate cells, although in small quantities, except in Punica and Ceratonia. In the case of Justicia carnea only, Sanio states that he found the cells containing air, 'no doubt abnormally.'

b. Sanio's *intermediate cells*[1] (Ersatzfaserzellen) (Fig. 205, p. 480), agree with the short-celled parenchyma of the ligneous bundles which will be next described, in all

[1] [In justification of the use of the term 'intermediate cells' in place of a more strict translation of the term 'Ersatzfaserzellen' introduced by Sanio, it may be pointed out that, though the intermediate cells do replace the short-celled parenchyma in some few cases, that is not their constant character. It is thought that the use of the term 'intermediate cells' will avoid this difficulty, while it brings the real character of the cells more prominently forward, viz. that they are intermediate in *form* between fibrous and short parenchymatous cells; compare Sach's Textbook, 2nd Engl. Ed. p. 950]

[2] A. Braun, *l. c.*; compare p. 471.

properties, with the exception of their shape, and the form of their pits, which in many species is not rounded but slit-like. Sanio's term owes its origin to the fact that they not only frequently accompany the short-celled parenchyma of the bundle, but in many woods exclusively represent or *replace* it, as in Viscum, Porlieria, Caragana arborescens, and Spiræa salicifolia.

2. The *short parenchymatous cells* of the wood present some differences according as they belong to the ligneous bundles or to the medullary rays. Thus the *parenchyma of the bundles*, usually called '*wood parenchyma*,' is to be distinguished from the *parenchyma of the rays*.

The parenchyma of the bundles has been principally investigated in the case of hard woods, and it is to these that most of the following statements apply. They may, however, with some obvious modifications, be also extended to the soft, fleshy, succulent, or at least loose woods, which consist chiefly of parenchyma, as in the stems of Papayaceæ, Bombax, and Chirostemon, and in many roots.

The cells of the typical parenchyma of the bundles arise by predominant transverse divisions of the elongated tissue mother-cells in the cambial zone. Accordingly they are arranged in simple, or in some places multiple, longitudinal rows, each of which has a somewhat spindle-shaped form, resembling that of the mother-cell. This grouping comes out most conspicuously when they lie isolated in non-equivalent tissue, less so where they are united to form larger masses. The length of the spindle-shaped groups is usually less than that of the fibrous cells, more rarely, as in Vitis, it is on the average equal to it.

The form of the individual cells is that of a more or less elongated prism, with horizontal or oblique terminal surfaces; it is obvious that those which form the ends of a group must further show a conical tapering. Those which border on wide vessels are often flattened in the direction of the circumference of the vessel, and elongated transversely, in consequence of the expansion of the members of the vessel at the expense of their surroundings (p. 470).

In many cases the cells which surround a group of contiguous vessels on opposite sides are connected by means of flatly tubular outgrowths of their lateral walls, which penetrate between two vessels, and fit on to one another at their ends. The outgrowths are frequently branched, frequently they have blunt ends without fitting on to others. This phenomenon is explained by Sanio [1], and no doubt correctly, by the unequal growth and partial displacement of single rows of parenchymatous cells originally lying between the rudiments of the vessels. It occurs in Casuarina, Melaleuca imbricata, Platanus occidentalis, Celtis australis, Ficus Sycomorus, Cordia pallida, and especially in Tectona grandis and Avicennia spec.; and it has also been found by Sanio in the intermediate cells of Porlieria.

The wall of the parenchymatous cells of the bundles is in the harder woods always provided with roundish or elliptical pits which are not bordered; they are never slit-shaped, or arranged in regular oblique rows; on the sides which are in contact with vessels they are usually larger than on the others, though exceptions to this rule occur (Betula alba). The pitting goes all round, even over the transverse walls, and the latter are of equal thickness with the lateral, or the thinner lateral walls—a point of

[1] *L.c.* p. 94, where the further details are to be compared.

distinction from the septate fibrous cells. The walls, though lignified in the mature condition, are uniformly distinguished from those of the tracheæ and fibres of the same wood by their lesser thickness. Exceptions to this rule are very rare: Magnolia acuminata and tripetala, Liriodendron tulipifera, Gymnocladus canadensis, and Amorpha fruticosa, in which the radial walls of those woody parenchymatous cells which lie in the autumn wood are not inconsiderably thickened. Spiral or annular fibres are always absent. The parenchyma of the bundles in soft fleshy woods is in general only distinguished from that above described, by its usually larger cells, and less thickened walls.

The nature of the cell-contents is in general characterised by the term parenchyma. In most hard woods the starch-grains, which are stored up periodically, during the winter's rest, form the chief contents; chlorophyll and tannin occur here and there; the former, for example, in the wood of Cobæa scandens.

The parenchyma of the *medullary rays* consists, in the great majority of secondary woods, of cells which have essentially the same properties as the parenchyma of the bundles in the same plant, without being exactly similar in every point. In woods which are not fleshy and succulent the walls of the cells of the medullary rays are as a rule lignified, like those of the woody parenchyma. Exceptions to this rule occur in many twining and climbing plants, in which the cells of the medullary rays remain unlignified, delicate, and capable of yielding to pressure and tension, e. g. Menispermum canadense, Aristolochiæ, Atragene alpina. The lignified medullary rays of Clematis Vitalba, which agrees so closely in every respect with Atragene, show however that this phenomenon is by no means generally characteristic of plants with the habit mentioned.

The form of the cells of the medullary rays is usually that of a rectangular prism, often with rounded corners, and roughly comparable to a brick; in thin medullary rays, filling up a narrow mesh between the ligneous bundles, the cells which occupy the angles of the mesh have a corresponding wedge-like form. Usually the cells are chiefly elongated in one direction, and are either *procumbent* with their greatest diameter directed horizontally and radially; or *upright*, with their greatest diameter vertical. The former is by far the most frequent case. Cells standing vertically occur, for example, in Asclepiadeæ (Periploca, Hoya, Asclepias curassavica), Nerium, Drimys Winteri, and Medinilla farinosa. In the medullary rays of Camellia japonica procumbent and vertical cells occur in groups. Medullary rays with procumbent cells are always easy to distinguish from parenchyma of the bundles, even where they traverse the latter, because the longitudinal diameters of the two kinds of cells cross one another; in the case of the upright cells this distinction is often less simple on account of the similar direction of the longitudinal diameters.

But few minute investigations on the structure of the cells of the medullary rays exist, and many details are still to be discovered. From what is already known, it may however be asserted that the cells of a medullary ray are as a rule similar to one another, apart from irrelevant differences, some of which follow directly from what has been said. But few exceptions to this rule are known. In the medullary rays of Aristolochia Sipho, Sanio[1] found smaller cells, containing finely granular starch, arranged in

[1] *L. c.* p. 127.

irregular reticulate rows, between larger, empty, dried-up cells, a condition which recalls the pith of the Roses, &c. In the medullary rays of Atragene alpina annular zones of two kinds alternate from within outwards, the one consisting of a few rows of relatively narrow, closely connected cells, the other of somewhat larger cells connected to form an irregular, coarsely lacunar tissue, but otherwise similar in structure to the narrow cells. This structure owes its origin to the fact, that with each thickening of the ligneous bundles the medullary ray receives an increment of growth, which remains on the whole smaller in the radial direction than that of the ligneous bundles as regards the number and size of its cells. Certain cells or groups of cells either follow the general growth, or are dragged apart in a purely mechanical manner in consequence of it, so as to form the lacunar zones. In general, though not exactly, each pair of dissimilar zones corresponds to an annual ring.

In the wood also the cells of the parenchyma are no doubt always accompanied at least by narrow intercellular interstices containing air. In particular cases, to be mentioned below, they surround wide passages containing secretions.

Sect. 145. Forms of tissue other than those discussed in the preceding paragraphs are in most woods either absent, or, at any rate, of small importance. The most widely distributed are the *sacs containing crystals*, which, wherever they occur, accompany the parenchyma of the bundles or of the medullary rays; e.g. Leguminosæ, as Pterocarpus santalinus, Hæmatoxylon[1], Herminiera (pp. 139 and 141), Vitis, &c.

Laticiferous tubes are abundantly developed in the wood of the Papayaceæ, which is chiefly parenchymatous. Their reticulately connected branches are here distributed between the elements of the parenchyma, and are in contact with the vessels. In other plants containing latex, only those branches which run from the cortex into the pith pass through the secondary wood. No doubt they always exist earlier than the latter, from the primary differentiation of tissues onwards, and subsequently become enclosed, and also of course stretched, by the secondary growth. Where one of these connecting branches borders on woody fibres, the latter are not uncommonly bent inwards so as to follow its course, as is indicated in Fig. 190, p. 438, by the oblique shading. Comp. also Chaps. VI and XII.

The classification of the elements of the secondary wood given in Sects. 141–145 is based on that which Sanio, in agreement with T. Hartig[2], has given in his fundamental works cited above, p. 478. It differs, however, from the latter in some points. Apart from the medullary rays, Sanio classifies the elements of the ligneous bundles as follows:—

I. Parenchymatous System.
   1. Woody parenchyma.
   2. Fibres representative of the woody parenchyma.

II. Libriform System.
   3. Simple undivided bast-like wood-cells or wood-fibres: *Libriform* tissue.
   4. Septate Libriform tissue.

III. Tracheal System.
   5. Tracheides.
   6. Vessels.

His System II includes both our woody fibres and our fibrous cells, the two are placed together on account of their form and the structure of their walls, while no primary

[1] Flückiger and Hanbury, Pharmocographia, pp. 176, 188.
[2] Compare especially Botan. Zeitg. 1859, p. 92.

importance is attached to their contents. The intermediate fibres are separated from the fibrous cells, also on account of the structure of their walls, and placed, with the parenchyma of the bundles, in Category I. The rest of the classification resembles our own. In so far as nothing further is aimed at than an intelligible arrangement of the forms of tissue of the secondary wood, Sanio's classification is without doubt as intelligible as our own, and perhaps more so. Both also suffer from the same defect, namely, that the categories distinguished cannot always be sharply separated, and in particular that intermediate forms occur between fibres and tracheides, &c., as has often been stated above. Both, however, afford guidance in each particular case, in accordance with the system adopted. There would therefore be no reason for undertaking alterations in Sanio's arrangement, if it were not an essential object to refer the forms of tissue in the secondary wood to their proper place among those distinguished in the plant generally, including those outside the secondary wood. It can admit of no doubt that the elements of the secondary wood are not organs *sui generis*, but belong to the forms of tissue which have been characterised in this book as tracheæ, sclerenchymatous fibres, and cells; the last being distinguished from the others by permanently containing protoplasm, or in doubtful cases by their periodically varying store of starch (comp. pp. 5 and 115). The known phenomena of the secondary wood present, as I believe, no argument against the general classification of the forms of tissue carried out in this book, for the occurrence of intermediate phenomena cannot avail as an argument against the distinction of typical forms. In the face of these facts it was, however, necessary to depart in some points from Sanio's classification, which was based on other considerations.

I willingly grant that the sharp separation of the cells from the other elements is often inconvenient for the practical description or identification of woods, as it is not always an easy matter to establish the cellular quality. In most cases indeed the presence of starch is a certain character, both in the fresh and in the dry wood. In its absence, however, the distinction is in the latter often impossible or only possible with great difficulty. In the wood of Cobæa, for example, which has been preserved dry, it can scarcely be determined with certainty whether the numerous reticulated elements with large pits are short tracheides or parenchymatous cells, for in the structure of their walls they resemble reticulated tracheæ, which might occur, and all the formed contents have become indistinguishable. In the fresh plant, on the other hand, the presence of protoplasm and with it the cellular quality may be recognised, at least up to the third year, by means of the large chlorophyll grains. Experiences of this kind are, as we have said, inconvenient, though, on the other hand, they are certainly instructive, as they point to the necessity of investigating woods in the fresh living condition, more than is usually done. They would, however, only present a serious objection to the classification arrived at, if the problem of the anatomy of wood were to be sought in the construction of a convenient 'key' for description and identification.

3. *Distribution of the tissues in the wood.*

Sect. 146. The distribution of tissues in the wood, and the consequent structure of the latter, is uniform in the successive annual rings, with the exception of certain differences to be specially treated of below; the single annual ring may therefore be considered first. In the few cases without annual rings the description applies to the entire woody ring.

As has already been often mentioned, alternate radial bands of unlike structure are nearly always apparent at the first glance: (1) the medullary rays, and (2) the ligneous bundles. This fact determines the main subdivisions of the exposition. Where this alternation of unlike radial bands does not exist, as in the cases men-

tioned on p. 458, and in many fleshy roots to be mentioned below, the entire mass of secondary wood is to be regarded as a single cylindrical ligneous bundle.

a. *Medullary rays and medullary spots.*

Sect. 147. In the woods which have been principally investigated, every zone possesses a large number of medullary rays of various rank. Since new secondary ones always arise as the ligneous mass grows in thickness, their number increases with that of the successive layers. And further, as in the successive layers their size either remains approximately uniform, or at least increases in a much lower degree than their number, it may well be assumed that the proportion between the space occupied by them, and that occupied by the ligneous strands, remains approximately the same in all the successive layers. This assumption agrees with the observation that where the increase in number of the medullary rays is very slight, an especially striking dilatation of the original ones occurs; e. g. Atragene. No detailed researches on this relation exist.

The number of the medullary rays in the surface of cross-section is apparently about in inverse proportion to their size, i. e. to their breadth, and no doubt their height also. Nördlinger[1] undertook a great number of enumerations, which, although according to his own judgment they are not exactly reliable for woods with numerous medullary rays, on account of the serious difficulties, and are also taken from casually selected annual rings, yet give definite proportional numbers for the very different conditions obtaining in the particular species. He gives, for example, in a breadth of 5 millim., for Aristolochia Sipho 9, Clematis Vitalba 10, Cytisus Laburnum 19, Robinia pseudacacia 20, Acer pseudoplatanus 33, Abies pectinata 37, Abies excelsa 44, Acer platanoides 47, Acer saccharinum 53, Quercus pedunculata 64, Alnus glutinosa 78, Æsculus rubicunda 84, Euonymus europæus, Punica Granatum 105, Rhododendron maximum 140 (the highest figure determined). The average *breadth* of a medullary ray varies according to the species, by Nördlinger's measurements (*l. c.*), from 1 mm (Quercus Cerris) to 0·015 mm (Æsculus, Buxus, Castanea, Euonymus europæus, Hamamelis, Juniperus communis, virginiana, Kœlreuteria, Ligustrum vulgare, &c.). It amounts to about 0·025 mm, according to the same author, e. g. in Abies pectinata, Pinus, Larix, Taxus baccata, Syringa vulgaris, &c., to about 0·05 mm in Acer pseudoplatanus, dasycarpum, Juglans, Robinia pseudacacia, Sambucus nigra, &c., to about 0·1 mm in Ailantus, Alnus incana, Cytisus Laburnum, Gleditschia, Platanus acerifolia, &c. Whether the measurements were made on sections of sufficient thinness for the determination of absolutely exact numbers may remain undecided.

The *height* of the medullary rays is not less variable in different species than their breadth, but has received much less attention in the published investigations. In woods without intermediate bundles, and in Clematis with one intermediate bundle to each primary one, the height of the primary rays is equal to that of the internodes, and thus amounts to 100 or 200mm. In the smallest secondary rays of the Abietineæ, which are only 1–2 cells high, it scarcely exceeds 0·025 mm.

[1] Querschnitte von Holzarten, Band 2, p. 5.

These relative magnitudes may be better determined according to the number of cells, or layers of cells, which compose the medullary ray in breadth and height, than according to absolute measurements. Those under 0·025 mm in breadth are no doubt all of them only one cell broad (at most two or a few in the middle), and are thus 'uniseriate' as seen in tangential or transverse section, as, for example, in almost all Coniferæ, and generally in the narrowest of the above examples; while in like manner the broader ones are always pluri- or multiseriate. Similar rules obviously hold good for the relative heights, and here also the number of cells varies, according to the particular case, from very high figures, down to one or two.

Certain woods possess medullary rays of *two different* sizes, with which differences of the minute structure are also usually connected; e.g. those of the Abietineæ, to be described below, which differ in the presence or absence of a resin-canal; the broad high multiseriate rays, and numerous low uniseriate ones between them in Quercus and Fagus; small secondary rays, which are triseriate in the middle, between the much larger primary ones, in Casuarina[1], &c.

The medullary rays are sharply defined, and exactly fill the meshes between the ligneous bundles, which run in a curved course around them. An exception to this rule is described by Schacht[2] in the case of the wood of the root in Araucaria brasiliensis, in which the uniseriate rays, consisting of irregularly undulated cells, are united by rows of similar cells, which run between the tracheides of the ligneous bundles vertically, from one ray to another, lying above or below it. A further exception is formed by the *medullary spots* to be described below. In the great majority of cases the medullary rays consist only of parenchyma. In many woods they collectively constitute the main mass of the parenchymatous tissue which is everywhere distributed between the other elements: in many cases (Wintereæ) this is represented by them alone, in others (Coniferæ) at least to much the greatest extent. The succulent parenchyma, which forms the greater part of the wood of the stem in Carica and Vasconcella, is principally formed by the large-celled, broad, and high medullary rays.

Exceptions to this purely parenchymatous structure rarely occur. As such are to be mentioned in the first instance the medullary rays of many *Abietineæ*, all investigated species of Pinus in the narrower sense, Cedrus, Larix, Tsuga canadensis, Abies excelsa, and balsamea—and of Sciadopitys, which consist of *two kinds* of elements, namely, parenchymatous cells, and *tracheides* of similar form to the latter, distinguished by Hartig[3] as 'fibres.'

Among the Abietineæ, the Pines (Pinus), Firs (Picea excelsa), Larix and Pseudotsuga, have two kinds of medullary rays: larger ones, which contain, in their many-layered central portion, a resin-canal which runs horizontally into the bast, and is not in communication with other canals of the wood and bast[4], and smaller single-layered rays, usually only a few (1–12) cells or elements in height, and destitute of a resin-canal. The other trees mentioned have medullary rays of only one kind, and of the structure last mentioned;

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[1] Compare Göppert, Linnæa, Bd. XV. p. 747.—Löw, Diss. de Casuarinearum . . . . Structura, Berl. 1865.

[2] Botan. Zeitg. 1862, p. 412, Taf. XIII. 15.

[3] Forstl. Culturpfl. p. 13, Taf. V. Compare also his Jahresber. (1837), p. 145.

[4] Hartig, Naturgesch. d. forstl. Culturpfl. p. 95, Taf. 5.—Von Mohl, Botan. Zeitg. 1859, p. 334.

they seldom exceed the height and breadth stated;—in Cedrus they are as much as 50 cells in height, and often more than one cell broad in the middle. In the species first mentioned above, the medullary ray consists firstly of somewhat elongated, prismatic, procumbent *cells*, which, on their surfaces of contact with one another and with the tracheides of the ligneous bundles, have, according to the species, one or more large, unbordered pits; in the latter case they are really not pitted, in so far as the thickening and the pit, strictly speaking, only belongs to the tracheide [1].

Secondly, *tracheides* occur in addition to these cells of the medullary ray, which they resemble in form and position. Their walls, where they border on equivalent elements, and on tracheides of the bundles, have bordered pits of smaller size than those of the latter; in many species of Pinus (e. g. P. silvestris, and Laricio), and Sciadopitys, they further have irregular thickening ridges, projecting inwards like teeth, on their upper and lower sides; towards the cells of the medullary ray they only have extremely scattered small pits, which, so far as I could see in P. silvestris, are unbordered. Each of the radial rows of which the medullary ray consists, is, as far as investigation extends, composed exclusively of one of these two kinds of elements, and in fact in a ray more than two elements in height, the upper and lower wedge-shaped edges always consist of one to three series of tracheides. In the middle of the medullary ray there then lie either rows of cells only, or rows of tracheides alternating with the latter. E. g. they occur in the following order, succeeding one another from above downwards (or conversely), the Roman numerals indicating the rows of tracheides, the others the rows of cells, and the letters (*a*), (*b*), &c. the particular medullary rays investigated.

Pinus silvestris, wood of the stem: (*a*) II, 4, I, 1, II. (*b*) I, 2, I, 3, I. (*c*) I, 3, IV, 3, II. (*d*) I, 2, I. (*e*) II, 4, I, &c.

Larix europœa, stem: (*a*) I, 1, II, 6, I. (*b*) I, 1, IV, 9, I. (*c*) I, 14, I, &c.

Small medullary rays, only two elements in height, are in P. silvestris often composed of tracheides only [2].

The second exception to the usual, purely parenchymatous structure, occurs in several plants which form but little wood, and consists in the fact that the medullary ray is not formed of parenchyma, but of elongated, sclerotic *fibrous cells*. It has been primarily observed in the perennial stems of the suffrutescent Begoniæ [3], e. g. B. angularis, muricata, Hügelii. The very large and broad medullary rays of the secondary wood here consist of upright, very much elongated cells, which abut on one another with oblique, sometimes acute, sometimes blunt, terminal surfaces, very like the cambial cells of the ligneous bundles, and acquire lignified, sclerotic walls of considerable thickness, with small pits. The cells have scanty contents, and frequently even contain starch. The broad medullary rays form collectively a tough ring into which the relatively narrow ligneous bundles are fitted.

A similar structure occurs in many herbaceous stems of Umbelliferæ, as in Chærophyllum, Myrrhis, Seseli, Daucus, and Eryngium [4], though here more minute investigation is needed, with reference to some doubtful points suggested by Jochmann; it perhaps occurs frequently in herbaceous Dicotyledons. Of the cases adduced by

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[1] See Fig. 58, p. 159. Further, Hofmeister, Pflanzenzelle, p. 175.—Sanio, in Pringsheim's Jahrb. VIII.

[2] For further details see Kraus, Bau d. Nadelhölzer, Würzburger Naturwiss. Zeitschr. Bd. V.—Göppert, Monogr. d. Fossilen Coniferen, Harlem, 1850. For figures see especially Göppert, *l. c.*; also Schacht, Baum, 1 Aufl. p. 202; Lehrbuch, I. p. 233.

[3] Hildebrand, Begoniaceen-stämme, p. 24.

[4] Jochmann, Umbelliferarum Structura, p. 10.

Schwendener (Mechan. Princip, p. 148, sub. 3), Tropæolum, Impatiens, Centranthus, and Cachrys, *perhaps* belong to this category, the others not.

In any case all the exceptions of the category last-mentioned constitute transitional forms to those mentioned at p. 458, where there is no sharp lateral limitation of distinct ligneous bundles by radial bands of non-equivalent structure, and hence medullary rays cannot be distinguished at all, whether it be that only the large medullary rays are absent and small secondary ones appear later, as in Ephedra and Cobæa, or that rays of every rank are absent throughout, as in Crassulaceæ, Centradenia, Rumex Lunaria, and Campanula Vidalii.

Sect. 148. In many woods, e.g. constantly in species of Alnus and Sorbus, accumulations of parenchymatous cells occur, constituting as it were local hypertrophies of the medullary rays; these were first described by T. Hartig as *cellular passages*, subsequently by Nördlinger as *medullary spots*, and by Rossmässler as *repetitions of the pith*. According to the investigations of these authors and of Kraus[1], these structures appear in cross-section in the form of elongated spots, usually at the outer side, but not unfrequently in the middle of an annual ring, with their greatest diameter following the periphery of the ring, while they often form considerable annular segments extending through 90° and more. In the vertical direction they extend like passages for distances of several feet, sometimes ending blindly, sometimes branched here and there, not unfrequently crossing one another in their irregular course. They are often conspicuous to the naked eye by their brown colouring, e.g. in the trees mentioned; in other cases they are colourless, e.g. Populus monilifera, and tremula. They consist of irregularly polyhedral, irregularly arranged cells, with thick pitted walls, contents including starch, tannin, &c.; the latter are generally brown in the dry wood, and chiefly contribute to the colouring of the spots. This may also partly depend on very thin-walled, compressed (partly disorganised?) cells at the circumference of the spot, as described by Kraus in the case of Sorbus torminalis. They owe the names given them to the similarity of their thick-walled cells to those of the pith, especially of its periphery. The medullary rays coming from the middle of the stem enter the inner side of the spots, their cells becoming broader as they approach the latter, and assuming more and more the characteristics of those of the spots; thus the medullary rays pass over from within outwards into the passages; they further coalesce with them laterally. On the outside new medullary rays start from the passages, and as regards their direction these are either independent of those coming from within, or lie in the same straight line with them. Local swellings of the medullary rays, due to increased breadth and number of their cells, which latter may assume irregular forms, are immediately connected in structure with the smaller spots or passages of this kind; and this also applies to the longitudinal union of neighbouring rays, by means of small groups of parenchymatous, more or less irregular cells, which abut on them. Such structures occur in Abies alba, balsamea, Pichta, in Cunninghamia, Cupressus sempervirens, and frequently also in Abies pectinata. In the Coniferæ, and in Liquidambar, hysterogenetic and lysigenetic resin-

[1] Hartig, Forstl. Culturpflanzen.—Nördlinger, Querschnitte, Bd. II.—Kraus, Nadelhölzer, *l. c.* p. 162.

canals often arise in them[1]; in the wood of Prunus avium, they are, according to Wigand[2], a principal starting-point of the disorganisation which produces the cherry-gum.

The dilatations of the medullary rays and the medullary spots occur, it is true, relatively seldom; they are, however, characteristic of many woods, both Dicotyledonous and Coniferous. According to Kraus and Nördlinger they have been frequently observed in Betula alba, dahurica, populifolia, Cratægus oxyacantha, monogyna, pyracantha, cordata, Cydonia vulgaris, Pyrus prunifolia, Amygdalus communis, Cotoneaster microphylla, Prunus spinosa, Salix aurita, Caprea, bicolor, Rhus Cotinus, Lühea grandifolia, Pterocarya caucasica, Vaccinium Myrtillus, Vitex incisa, Calluna vulgaris, Erythroxylon grandifolium, Guazuma ulmifolia, and Liquidambar styraciflua, besides the plants mentioned above; while they occur rarely in Alnus viridis, Catalpa, Magnolia acuminata, and Salix triandra. I leave unmentioned the cases marked (?) by Nördlinger. Among the Coniferous woods Kraus found them in Abies balsamea, Pindrow, Pichta, Picea orientalis, and Juniperus excelsa; in Abies pectinata, Cedrus Deodara and Larix, he only found swellings of the medullary rays. In Dicotyledonous woods the passages occur chiefly in the lower part of the stem, and are thence continued into the roots; they also extend, however, into the apices and branches, though here they are less numerous and constant. In the Coniferous woods their course has not been minutely investigated; according to Dippel's statements (*l. c.*), which concern this particular point but little, those in the white Fir which contain resin canals may be traced longitudinally for considerable distances.

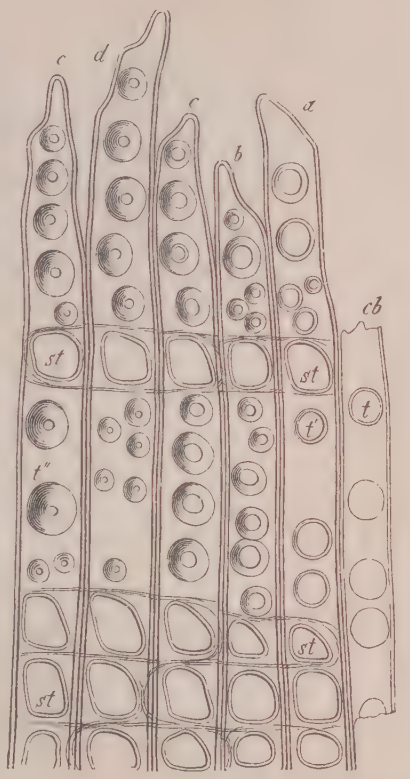

FIG. 208.—Pinus silvestris; radial longitudinal section through the wood of a branch. *a—e* ends of tracheides, with bordered pits (*t'*, *t''*) in superficial view; *cb* portion of the young wall of a tracheide with bordered pits still immature; the further development of the latter and the contraction of the canal in the succession *a—c*; *d*, *e* mature condition; *s*, *t* large pits on the boundary between tracheides and cells of the medullary ray (550). From Sachs' Textbook.

b. *The ligneous bundles.*

SECT. 149. The structure of the ligneous bundle within an annual ring differs according to the presence or absence of the particular forms of tissue, and according to the distribution of those which are present, and the form and structure of each

[1] Kraus, *l. c.*—Dippel, Botan. Zeitg. 1863, p. 253.
[2] Pringsheim's Jahrb. III. p. 118.

element individually. In addition to these there are differences, to be discussed below, which are presented by the structure of the same form of tissue in the spring and autumn wood, and by the general grouping of all the elements of the ligneous body.

1. In some few woods the bundles are composed of only *one* form of tissue, to the exclusion of all the rest, and they then consist of *tracheides*, which, apart from the general differences between spring and autumn wood, have everywhere the same structure. In these cases the parenchymatous system is represented only by the medullary rays, which are inserted everywhere in great numbers between the bundles. Among Dicotyledonous woods the *Wintereæ* belong to this category; namely, Drimys Winteri and its allies, Tasmannia aromatica[1], and Trochodendron aralioides[2], the systematic position of which is doubtful: among *Coniferæ*, Taxus baccata belongs here, according to Sanio, but in the case of this tree Hartig and Kraus state that scanty bundle-parenchyma is present.

In the other Coniferæ the *tracheides*, of which the main mass of the wood is

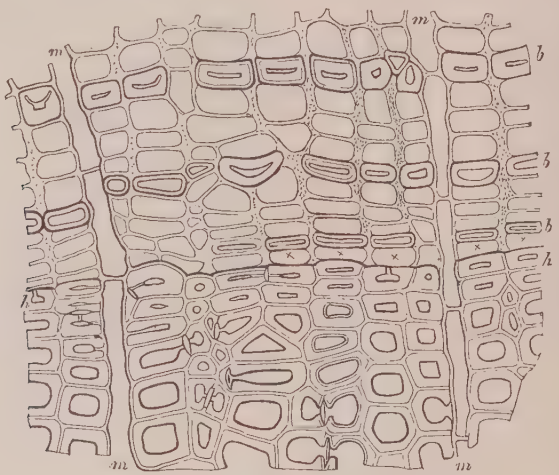

FIG. 209.—Juniperus communis; stem; cross-section through the autumn wood, bast, and cambium during the winter's rest (end of September). *h—h* outermost series of the autumn wood; *b*, *b* series of bast-fibres. At × there is only one cambial cell between *h* and *b*; *m—m* medullary rays.

homogeneously composed, are accompanied by bundle-parenchyma, which sometimes occurs in single vertical rows, scattered among the tracheides, while sometimes, as in many Abietineæ, it forms the coating of the resin-canals.

In the Coniferæ (Figs. 208 and 209) and the other plants just mentioned, the tracheides are arranged in radial rows; they are quadrangular, as seen in cross-section, when those which belong to neighbouring radial rows stand opposite to one another, hexagonal or pentagonal when the radial rows are alternate; their ends are elongated and sharp, owing to inclination of the radial surfaces (comp. p. 469). The radial surfaces have large corresponding bordered pits, which in the Wintereæ, the Araucariæ, Dammaræ, and the wood of the root in other Coniferæ, form two or more longitudinal rows, while in the

[1] Göppert, Linnæa, Bd. XVI. p. 134.—Kraus, *l. c.*
[2] Eichler, in Flora, 1864, p. 451.

stem-wood of the rest of the Coniferæ they form only a single longitudinal row, apart from individual exceptions, which are frequent, for example, in Larix. In the Coniferæ pits only occur on the tangential surfaces in the autumn wood. Taxus, Cephalotaxus, and Torreya further show spiral or annular thickenings on the inner surface of the wall of the tracheide[1]. Comp. Chap. IV.

The resin-canals, surrounded by parenchyma as epithelium, occur in the ligneous bundles of the same Abietinæ which possess horizontal canals in the medullary rays (p. 490). They run longitudinally, and, as seen in transverse section, lie scattered in a ring in the external region of every annular layer. Their number varies according to species and individual; Von Mohl[2] counted, for example, on an equal transverse surface embracing several annual layers, in Pinus nigricans 190, P. silvestris 124, Larix europæa 128, Picea excelsa 78.

2. The ligneous bundle of all Dicotyledonous woods, except those mentioned above, and of the Gnetaceæ (Ephedra, Gnetum) always contains vessels, and at least one of the forms of cells distinguished; of the latter bundle-parenchyma and intermediate fibres are usually present together. These are further accompanied, according to the species, by some or all of the other tissues characterised in Sects. 142–144. Of the combinations thus possible, the following have been demonstrated, according to Sanio's statements, in the trees and shrubs investigated.

1. *Vessels, Tracheides, Bundle-parenchyma, Intermediate fibres.*

(*a*) Only with bundle-parenchyma: Ilex Aquifolium, Staphylea pinnata, Rosa canina, Cratægus monogyna, Pyrus communis, Spiræa opulifolia, Camellia, &c.

(*b*) Only intermediate fibres: Porlieria.

(*c*) Both forms of cell: Jasminum revolutum, Kerria, Potentilla fruticosa, Casuarina equisetifolia and torulosa, Aristolochia Sipho, and many others.

2. *Vessels, Tracheides, Fibrous cells, Bundle-parenchyma, Intermediate fibres.*

(*a*) Only bundle-parenchyma: fibrous cells non-septate: e. g. Sambucus nigra, racemosa, Acer platanoides, pseudoplatanus, campestre.

(*b*) Bundle-parenchyma and intermediate fibres, fibrous cells non-septate: Ephedra monostachya, Berberis vulgaris, Mahonia[3].

(*c*) Bundle-parenchyma, fibrous cells septate and non-septate: Punica, Euonymus latifolius, europæus, Celastrus scandens, Vitis vinifera, Fuchsia globosa, Centradenia grandifolia, Hedera Helix, &c.

(*d*) All four forms of cell: Mühlenbeckia complexa, Ficus (?).

3. *Vessels, Tracheides, Woody fibres, Bundle-parenchyma, Intermediate fibres.* This is the prevalent, one may almost say the typical, combination.

(*a*) Only bundle-parenchyma: Sparmannia africana, Calycanthus, Rhamnus cathartica, Ribes rubrum, Quercus, Castanea, Carpinus spec., Amygdaleæ, Melaleuca, Callistemon spec., &c.

(*b*) Only intermediate fibres: Caragana arborescens.

(*c*) Both forms of cell. Most Dicotyledonous woods no doubt belong to this series, e. g. Salix, Populus spec., Liriodendron, Magnolia acuminata, Alnus glutinosa, Betula alba, Juglans regia, Nerium, Tilia, Hakea suaveolens, Ailantus, Robinia, Gleditschia spec., Ulex europæus, &c.

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[1] Compare Hartig, Kraus, Göppert, *l. c.*—Von Mohl, Schacht, Botan. Zeitg. 1862.

[2] Botan. Zeitg. 1859, p. 340.

[3] Compare Sanio, in Pringsheim's Jahrb. IX. p. 55.

4. *Vessels, Woody fibres, Parenchyma, Intermediate fibres.*

(*a*) *Both kinds of cells:* Fraxinus excelsior, Ornus, Citrus medica, Platanus, &c.

(*b*) Only intermediate fibres: Viscum album.

(*c*) Only bundle-parenchyma: Avicennia.

5. *Vessels, Fibrous cells, Parenchyma.*

Cheiranthus Cheiri, Begonia. Here no doubt also belong many of the Crassulaceæ and Caryophylleæ which still need more minute analysis.

6. *Vessels, Fibrous cells, Parenchyma, Woody fibres* (?).

Coleus Macræi, Eugenia australis, Hydrangea hortensis.

7. *Vessels, Tracheides, Woody fibres, Fibrous cells* (septate), *Parenchyma, Intermediate fibres.*

Ceratonia siliqua, Bignonia capreolata, doubtful however as to the woody fibres according to the existing data.

Although no strict law holds good, without exception, for the distribution of these tissues in the woods containing vessels, still certain general rules may be given.

The *vessels* occur in all the layers of the annual ring, but are usually more frequent in the internal than in the external portion. Only Bombax Ceiba shows the opposite condition, according to Sanio. It is not uncommon, however, for their frequency to show no difference from within outwards (Acacia Sophora, floribunda, Enckea media, Artemisia Abrotanum); or only a slight one, the pores, or groups of pores which they present in cross-section, being scattered uniformly through the wood, e. g. Laurus nobilis, Æsculus, Acer, Populus. The vessels rarely form the main, fundamental mass of the wood (Avicennia). As a rule they lie in small groups in the non-equivalent fundamental mass, and these groups are either isolated or arranged in more or less interrupted radial bands or concentric zones (Hedera Helix). They are either everywhere of about the same width, or more usually their width is greater in the inner part of the annual ring, and diminishes gradually or suddenly towards the outside. With this difference in size, a difference in structure is in many cases also united, in so far as the narrow vessels have spiral fibres, while the wide ones have none (Morus alba, Broussonetia papyrifera, Gymnocladus, Virgilia lutea, Celtis australis, Ulmus suberosa, Catalpa, and Robinia pseudacacia); or the structure is the same in all (Quercus pedunculata, Castanea vesca, Fraxinus, Amorpha fruticosa, Sophora japonica, and Periploca).

In the above-mentioned 'parenchymatous' woods, as Bombax, Carica, &c., and also in the roots still to be discussed below, the *bundle-parenchyma* forms the main mass in which the vessels and other elements are inserted in groups. In the solid 'woody' woods its arrangement has a regular relation to that of the vessels.

It usually accompanies the latter, either in such a manner that it surrounds each vessel or group of vessels singly—paratracheal parenchyma according to Sanio, e. g. Enckea media; or it forms tangential bands, alternating with similar ones, consisting chiefly of tracheides or fibres, in or at the side of which the vessels stand: Sanio's metatracheal parenchyma. The latter, for example, is the case in the spring wood of Tectona grandis, in the autumn wood of Fraxinus, in the autumn and spring wood of Amorpha fruticosa, Sophora japonica, Robinia pseudacacia, Gleditschia triacanthos, Gymnocladus, Virgilia, Caragana arborescens, Paulownia, Morus, Broussonetia, Ailantus, Tamarix gallica, &c. In Casuarina equisetifolia, torulosa, Hakea

suaveolens, and other Proteaceæ, species of Ficus, Cordia pallida and many others, every annual ring has several concentric bands of metatracheal parenchyma.

According to Sanio, parenchyma always occurs scattered between the tracheides in Dicotyledonous woods, with the exception of Casuarina, where it only occurs in the metatracheal arrangement, and of Rosmarinus officinalis. It is absent between the typical woody fibres, according to Sanio, with the exception of Edwardsia grandiflora, Ulex europæus, Celtis australis, Olea europæa, and further of Hibiscus Rosa sinensis, where it actually forms tangential bands between the fibres. In Tamarix gallica it occurs even between fibrous cells which contain starch.

In some few cases of the wood of roots, which consists chiefly of masses of parenchyma, the latter are the seat of passages containing secretions: root of Inula Helenium[1] and Opoponax Chironium; Trécul's statement respecting Oenanthe crocata perhaps also refers to this subject[2].

For the *intermediate fibres*, the same rules hold good as for the bundle-parenchyma, because they occur either accompanying or representing the latter.

Although the *woody fibres* may occur in all the layers of the annual ring, they are present in especially large numbers in its central portion, in the case of hard woods. They here usually form the fundamental mass, in which the other elements, particularly vessels and parenchyma, are imbedded; in many woods, e.g. Robinia and Gleditschia, they occur only in the central portion of the ring, and are absent in the spring and autumn wood. In woods which are mainly parenchymatous (as Bombax and Cheirostemon), and in that of Avicennia, which chiefly consists of vessels, the fibres are only imbedded in small groups, or singly, between the elements of the fundamental mass.

For the *fibrous cells*, whether septate or non-septate (Berberis, Clematis, Vitis, Tamarix, Punica, &c.), the same rule of distribution holds good as for the woody fibres. As shown by the above statements as to their occurrence, the two elements, which are similar in form and in the structure of their walls, may mutually represent each other, indeed it is doubtful whether the case mentioned under 7, of the simultaneous presence of both, ever occurs.

The *tracheides* may likewise form by themselves the fundamental mass of the wood, representing, as it were, the two tissues last mentioned; this is the case in the combination mentioned above under 1, e.g. Pomaceæ, Camellia, &c. They then always belong to the 'fibriform' category, resembling woody fibres in shape, and in the character of their walls. Where, on the other hand, they occur in conjunction with fibres and fibrous cells, they are present chiefly in the neighbourhood of the vessels: and in fact they occur next them in small numbers, and isolated, when the latter are scattered singly or in small groups in the annual ring, and are all alike (e.g. Punica, Fuchsia globosa, Ceratonia, and Nerium). When, on the other hand, two kinds of vessels, distinguished by their size, and usually also by special structure, are present, then the tracheides accompany the small ones, rarely the large ones also (Quercus pedunculata, Castanea vesca, and Periploca). According to the mode of occurrence of the small vessels, they are then either distributed with the latter in the whole annual ring (Ulex

[1] See Berg, Atlas d. pharm. Waarenk. Taf. X.
[2] Trécul, *l.c.*; compare p. 448.

europæus, and Rosmarinus), or limited to its outer portion (Morus alba, Broussonetia, Catalpa, Paulownia, Sophora japonica, Gymnocladus canadensis, Robinia pseudacacia, Corylus, Carpinus, and Ostrya).—Secondly, the tracheides are in many cases most abundant in the outer part of the annual ring, or confined to it, even apart from their connection with particular vessels. In the annual ring of Ribes nigrum, Syringa vulgaris, Ligustrum vulgare, Euonymus europæus and latifolius, they successively increase in frequency towards the outer border of the annual ring, until they form the fundamental mass in which isolated vessels and fibres, or fibrous cells are imbedded; while in the inner portion of the ring the fundamental mass consists of fibres or fibrous cells, and the tracheides occur isolated, side by side with the vessels. Or the tracheides occur only at the outermost, autumnal limit of the annual ring, while the latter otherwise only contains vessels of one kind, as in Tilia, Salix hippophæfolia, acutifolia, Populus tremula, pyramidalis, Rhamnus Frangula, Juglans regia, cinerea, Pterocarya, Diospyros virginiana, Betula alba, Alnus glutinosa, Laurus nobilis, Camphora; Acer pseudoplatanus, platanoides, campestre; Sambucus nigra, and racemosa.

Sect. 150. Certain phenomena which depart in some degree from the usual rules, but belong nevertheless to the normal Dicotyledonous type, are here to be mentioned as special cases by way of supplement; they chiefly concern the wood of species or families which are distinguished by special adaptations, and by peculiarities of form correlated with these. Most of these phenomena still require more minute investigation, for which the following paragraphs will only contain indications.

We have, first, to return to the woods enumerated on p. 458 and p. 492, which are destitute of medullary rays. In those cases where only the primary large medullary rays are absent, while small ones soon appear, as Ephedra, Cobæa, and no doubt Xanthosia also, the above general rules for the structure and distribution of the organs hold good for the main mass of the wood. As far as the absence of the medullary rays extends in the cases mentioned, and in cases of their entire suppression throughout the whole secondary wood, the main and fundamental mass, with isolated exceptions to be mentioned below, consists of thick-walled fibrous cells or fibres—the latter being gradually developed from the former: these are usually elongated, though short in Echeveria pubescens, and have sharply pointed ends and a regular radial arrangement. Leaving out of consideration the xylem portions of the original leaf-trace bundles, which project into the pith, and belong to the medullary sheath to be described below (Sect. 152), the vessels—perhaps also series of tracheides of otherwise similar structure—and groups of bundle-parenchyma are inserted in the fundamental mass in the more strongly developed wood.

The grouping of the vessels and of the parenchyma, and the quantity and quality of the latter, vary according to the particular case. In the aërial stem of the *Crassulaceæ*[1] investigated, which has a somewhat strongly developed ligneous body, the parenchyma consists of elongated thin-walled cells, which remain unlignified, and accompany the vessels in longitudinal rows. The vessels and parenchyma are either quite isolated and scattered in the mass of fibres, at most two or three occurring together—Sedum maximum; or some of them form larger groups, consisting of as many as twelve elements—S. populifolium, and Echeveria

[1] Compare Brongniart, Arch. du Muséum d'Hist. Nat. tom. I.—Regnault, *l. c.*

pubescens; or they form with the parenchyma extensive groups, constituting transversely elongated, occasionally irregular, interrupted transverse bands—Sempervivum arboreum. Lastly, in the small creeping stems of Sedum reflexum, they form, together with the delicate cells, thick, multiseriate, continuous annular zones, which alternate with similar fibrous zones. Other species however, even those with thick stems, as Crassula lactea, Sedum ternatum, and Echeveria pubescens, form mere traces of secondary wood, which are scarcely worth mentioning.

In the *Caryophylleæ* investigated[1] (Dianthus, Gypsophila, Silene spec., and Arenaria graminifolia), especially in their rhizomes, thin-walled, long-celled parenchyma, often forming large irregular islets or annular segments, is inserted between fibrous masses of similar form, but in the foliage stems it may be absent, e. g. Gypsophila altissima. The vessels are numerous, and occur among both forms of tissue, often forming interrupted radial rows; in the fibrous groups they are often unaccompanied by parenchyma. In the foliage shoot of Dianthus plumarius the main mass of the very slight secondary thickening consists of vessels.

In the stem of *Rumex* Lunaria, the pitted vessels, accompanied by rows of bundle-parenchyma or by intermediate fibres, lie in very regular but interrupted radial rows in the fundamental mass, and the latter consists of fibrous cells densely filled with large starch-grains. With the exception of the starch, the same holds good for Centradenia grandifolia (comp. p. 484). In Campanula Vidalii the vessels are very isolated, and scattered in the radial series of fibrous cells, while I was unable to find any parenchyma or intermediate fibres accompanying them.

The *Rhinanthaceæ* require further investigation.

The secondary wood of the thicker, fleshy stems of *Cacteæ*[2] must again be mentioned here. The peculiar structure of the ligneous bundles, vessels, and tracheides, in the Mamillariæ, Echinocactus, &c., has already been repeatedly noticed above (comp. p. 478), and it must here be added, that in the genera mentioned the whole secondary ligneous bundle consists of the spirally and annularly thickened tracheæ, usually with a deeply projecting fibre, between which very thin-walled bundle-parenchyma is imbedded, in single longitudinal rows. The medullary rays of all ranks resemble the latter as regards the delicacy of their cells. In other Cacteæ, especially species of Cereus and Opuntia, the secondary ligneous bundle consists of tough woody fibres, and the scattered reticulated vessels which are usually accompanied by parenchyma (see p. 479). The parenchyma, including that of the medullary rays, may be very thick-walled and lignified, e. g. in Cereus speciosissimus. In the Opuntiæ short tracheides are also present, with the above-mentioned thickenings on the wall, which project inwards in the form of plates, and are usually annular. These elements are sometimes distributed singly in the interior of the bundle (O. tunicata, O. robusta), sometimes at its edges (O. cylindrica, ramulifera, andicola).

Lastly, the wood which forms the floating apparatus of the stems of certain Leguminosæ of the genera Æschynomene and Herminiera, which vegetate on the surface of the water, may deserve mention. Their structure appears to be very

[1] Regnault, *l. c.* p. 118, pl. VI.

[2] Compare Brongniart, *l. c.*—Schleiden, Anat. d. Cacteen, *l. c.* (p. 156).

uniform in the various species of these floating woods, as far as the existing descriptions extend[1]. Hallier's figures (*l. c.*) and Figs. 51–53 in Schleiden's Grundzüge (3 Ed.), I. p. 261, which at any rate represent a similar object, may serve to illustrate its coarser characteristics. The following short description refers especially to the wood of the Ambatsch of the White Nile (Herminiera Elaphroxylon = Ædemone mirabilis Kotschy[2]):—

The extremely light wood has no distinct annual rings. It consists, in its main mass, of elements which must be called tracheides (until undried material has been investigated), because in their condition as observed, they contain only air, without a trace of protoplasm or remnants of cell-contents. They stand alternately in radial rows, and have the form of hexagonal upright prisms, about three times as high as broad, with terminal surfaces inclined to the radial plane at an angle of about 45°, either unilaterally, or bilaterally, like a roof. Their thin colourless membrane is very beautifully thickened on the entire terminal surface, by a fine delicate network of fibres, while on the radial, and in a lesser degree on the tangential lateral surfaces, it is provided with small groups of simple minute pits.

The mass consisting of these tracheides is traversed (1) by very numerous parenchymatous medullary rays, containing starch, which are 1–10, on the average about six cells high and one cell in breadth, and further by some larger medullary rays, several cells broad in the middle; the cells of the medullary rays are elongated and procumbent. (2) By narrow bands arranged in irregular and often interrupted concentric annular zones, which are themselves crossed by the medullary rays; these bands chiefly consist of long-pointed fibres, with their ends overlapping one another, in a radially and tangentially oblique direction. In these bands, or more correctly on their inner (medullary) side, lie large pitted vessels, usually isolated, rarely forming short radial rows of few elements, and in both cases at long distances from one another laterally, being separated by several subdivisions of the wood, as determined by the medullary rays. Every vessel, or every group of vessels, is partly surrounded by a single layer of intermediate fibres containing starch, or by parenchymatous cells, with a moderately thickened pitted wall, 2–4 of which stand one above another; and very thin-walled, narrow parenchymatous cells, likewise containing starch, are continued in a single layer over the inner surface of each fibrous band. Between these the above-mentioned (p. 141) chambered crystal-sacs are here inserted. Tracheides, intermediate cells, members of the vessels, and also the medullary rays of medium altitude, are everywhere of approximately equal height, and lie with their ends in the same horizontal planes, thus forming regular horizontal layers. Their form and arrangement (with the obvious exception of the members of vessels) are similar to those usual in cambial cells, so that it may safely be assumed that they are derived from a cambial zone consisting of cells similar to them in height and form. The fibres, on the other hand, are (as estimated) at least double as long as the other elements mentioned, and must thus have undergone the corresponding elongation (and displacement) on their differentiation from the cambial zone.

c. *Changes of the individual forms of tissue in the annual ring.*

Sect. 151. In those of the cases just brought forward, in which the distribution of the forms of tissue is different in the successive layers of an annual increment of growth, and where the structure of the autumn-wood of one year is thus different from that of the neighbouring spring-wood of the next year, a limiting line must appear between

[1] Hallier, Botan. Zeitg. 1859, p. 152; 1864, p. 93.

[2] Compare Schweinfurth, Beitr. z. Flora Æthiopensis, p. 9.

the two. In addition to this cause of the demarcation of the annual rings, which consists in the distribution of non-equivalent tissues, and is not always present, there are two other causes, consisting in differences of form and differences of structure of equivalent tissue-elements, appearing in the successive, and especially in the extreme zones of an annual increment of growth.

The first of these phenomena consists universally, in a shortening of the radial diameter, and thus in a *tangential flattening* of the elements, at the outer limit of the autumn-wood, and this is due to increasing cortical pressure[1]. Changes in the average length may, as has been stated, be connected with this. The second cause, not present in all cases, consists in an increase in the thickness of the wall, and sometimes in further changes of its structure. These changes, especially the shortening of the radial diameter, affect both the elements of the medullary rays and those of the ligneous bundles. They come on either suddenly or gradually, and in fact this latter difference depends, partly on species, partly on differences in the vigour of development of the annual rings in one and the same wood.

These conditions are shown most simply and clearly in the woods of the *Coniferæ*[2], the bulk of which consists only of tracheides and medullary rays. In the procumbent elements of the medullary rays, the shortening of the radial diameter at the autumnal limit is not very conspicuous, though it does occur. The tracheides however are relatively wide at the spring limit of each annual layer, usually quadrangular as seen in cross-section, though sometimes pentagonal or hexagonal, and their radial diameter is equal to the tangential, or even somewhat greater; at the autumnal limit, on the other hand, they are always much flattened, i. e. the radial diameter is shortened. According to N. Müller[3], a diminution of their length in the autumn-wood is connected with this, in the case of the Fir. To this is further added an increase, accompanying the flattening, not only of the relative, but of the absolute thickness of the wall; and the appearance of pits on the tangential surfaces of the wall, while in the spring elements, with a wide lumen, the latter are limited to the radial surfaces.

By way of example, these conditions may be illustrated by the mean magnitudes found by Mohl[4] in the case of a well-grown specimen of Pinus sylvestris, thirty years old; they are expressed in Paris lines:—

		Spring-wood.	*Autumn-wood.*
Stem	Radial diameter	0·0204	0·0056
	Tangential	0·0142	0·0142
	Thickness of wall	0·0019	0·0031
Root	Radial diameter	0·0232	0·0094
	Tangential	0·0161	0·0161
	Thickness of wall	0·0018	0·0035

The sudden or gradual appearance of these differences, and the relative thickness of the zones with narrow and wide lumen, here depend in general on the thickness of the annular zones, as will be shown below.

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[1] H. de Vries, *l. c.* (p. 475).

[2] Göppert, Monogr. d. foss. Coniferen, *l. c.*—Von Mohl, Botan. Zeitg. 1862, p. 225, &c.—Kraus, *l. c.*

[3] Botan. Untersuchungen, IV. 2, p. 190.

[4] *L. c.* p. 237.

Deviations from the typical structure occur, in so far as groups of unusually thick-walled tracheides may appear in the different regions of the annular ring. These, as seen in cross-section, form band-shaped, annular segments, of a brownish yellow colour, similar to that of the autumn wood; in Pinus sylvestris they always occur in the innermost annual rings, and often also in the outer ones. Comp. Sanio, Pringsh. Jahrb. IX. 101.

In the *Dicotyledonous woods* the demarcation of the annual ring is further influenced by the distribution of non-equivalent forms of tissue, and of the changes which each of these shows in the successive zones of the annual ring.

The shortening of the radial diameter at the autumnal limit, sometimes occurring suddenly and sometimes gradually, and either amounting to a decided flattening or only occurring in a slight degree, according to the special case, is here also general: leaving out of consideration the vessels, which will be specially mentioned below, it is approximately uniform in the forms of tissue which occur in contiguity, more rarely it takes place to a very unequal extent: as in the marked and sudden flattening of the tracheides of the autumn-wood, while the radial shortening of the fibrous cells which accompany them is gradual and relatively much slighter, in Clematis Vitalba, and Mahonia Aquifolium.

With reference to the increase of the absolute thickness of the wall at the autumnal limit, a distinction must be drawn between the particular forms of tissue, for the latter differ from one another in average thickness in all the parts of any wood. In the case of equivalent forms of tissue both conditions occur, according to the kind of wood, namely, either a marked increase of the thickness of wall at the autumnal limit or its approximate constancy throughout. The latter, for example, is the case—

In the bundle-parenchyma of Gleditschia triacanthos, Ailantus glandulosa, Sophora japonica, and Caragana arborescens;

In the fibrous cells of Berberis, and Mahonia;

In the vessel-like tracheides of Betula, Alnus, Populus, Salix spec., Magnolia acuminata, Sambucus nigra, &c.;

In the thick-walled fibriform tracheides of Cornus sanguinea, Syringa vulgaris, and Buxus sempervirens.

Increase of the thickening of the wall at the autumnal limit takes place for example in—

The bundle-parenchyma of Gymnocladus, Morus alba, Broussonetia, Paulownia, and Amorpha fruticosa;

In the woody fibres of Laurus Camphora, Jatropha Manihot, and Carpinus Betulus;

In the vessel-like tracheides of Caragana arborescens, Carpinus Betulus, and Ostrya virginica;

In the fibriform ones of Syringa Josikæa, Philadelphus coronarius, Kerria japonica, &c.

Contrary to the rule holding good for other woods, Sanio observed a decrease of the thickness of the wall at the autumnal limit, in the tracheides of Staphylea pinnata, both as compared with the inner ones of the same annual ring, and with those of the spring-wood of the next following ring.

As regards the degree of increase in the thickness of the walls at the autumnal

limit, no accurate comparisons of the different forms of tissue have been carried out, but one may assume from the appearances, that it takes place in an approximately uniform ratio in all. Since then, as was shown above, the different forms of tissue of the same wood usually have a very unequal average thickness of wall, the total relative bulk of the walls at the autumnal limit must depend in the first instance on the distribution of the non-equivalent elements in the annual ring, and secondly on the increase of thickness, which has just been discussed, in each individual form of tissue. Thus, where, for example, the autumnal limit consists chiefly or exclusively of parenchyma, as in Morus alba, Broussonetia, Fraxinus, Robinia pseudacacia, Caragana arborescens, Amorpha fruticosa, Virgilia, Gleditschia, Catalpa, Paulownia, Ailantus, &c., or of vessel-like, thin-walled tracheides, as in Betula alba, Alnus glutinosa, Populus, Salix spec., and Cytisus Laburnum, while in the inner part of the ring thick-walled fibres prevail, then the autumnal limit is, on the average, thinner-walled than the next inner portion of the ring. The manifold possible combinations and modifications in this respect follow from what has been already stated.

The *Vessels* in most Dicotyledonous woods behave similarly to the other elements, in so far as they decrease on the average in width from the spring to the autumn limit of the annual ring, though without, as a rule, undergoing any conspicuous tangential flattening. With this a decrease in the number of the vessels from within outwards is often connected. Both differences may appear very gradually, as in the annual ring of the Salicineæ, Pomaceæ, Fagus, Buxus, Cornus sanguinea, &c., and may even be scarcely noticeable (Enckea media, Ulex europæus). In other woods, as Quercus pedunculata, Fraxinus, and Castanea, they appear suddenly, in such a manner that the first spring-zone of the ring, which is rendered highly porous by numerous very wide vessels, is succeeded on the outside by less numerous and much narrower vessels, occurring between the other elements. According to the degree in which this peculiarity of the spring-wood, which may be shortly characterised by the name 'porosity,' clearly appears, and coincides with other differences of structure between the annual limits and the middle portion of the ring, the boundary comes out more or less sharply even as seen with the naked eye. The trees last-mentioned form examples of especially sharp demarcation of the annular rings, and this is also the case with Fraxinus, Robinia pseudacacia and Gleditschia triacanthos, as the boundary is marked both by large vessels, and by the other conditions of structure mentioned above. If, on the other hand, the vessels, while of approximately equal width, are uniformly distributed singly or in groups, as in Enckea media, Ulex europæus, and no doubt Olea europæa also, the limit of the annual rings may be perceptible with difficulty, or scarcely at all, not only when slightly magnified, but even under microscopic investigation.

These various degrees in the demarcation of the annual rings, at once suggest the conjecture that cases of their entire suppression may occur. This unquestionably takes place as an individual peculiarity. Many plants, e. g. the Araucariæ, appear to have a special tendency to this, and such individual phenomena will be discussed below. Plants, in which the demarcation of the annual rings is constantly absent as a specific peculiarity, are certainly rare, and the statements respecting such cases have been so often disputed, that I am unwilling to adduce even those plants in which I was myself unable to find limits between annual zones,—namely the woody Piperaceæ, Opuntia,

Mamillarieæ and Cacteæ, and Cobæa scandens,—as certain examples of plants which are constantly destitute of annual rings[1].

Whether in tropical trees, as well as in our temperate zones, the annual ring as anatomically distinguished always represents the *yearly* growth, or whether there are trees with half-yearly rings, i. e. such as form two annual rings in the year, corresponding to the two periods of vegetation falling in one annual period, as has been stated to be the case in Adansonia digitata[2], appears to me to be a question which ought to be tested, but one that does not belong to the present anatomical exposition. Attention may here, perhaps superfluously, be recalled to the fact that in woods with alternating concentric bands of non-equivalent tissue, as Ficus, Casuarina, &c., markings are present, which resemble annual rings on superficial observation, but from which the true annual rings are distinguished by the characteristic structure of the autumn wood.

d. *Normal differences of successive zones of growth and annual rings.*

Sect. 152. The first innermost annual ring of every wood necessarily shows certain essential differences in its structure from all the later ones. In the stem, instead of the characteristic spring-wood, it has at its internal limit the groups of spiral, annular, and reticulated vessels (or tracheides) corresponding to the primary vascular bundles, but absent from the intermediate bundles; these usually project more or less into the pith, and, together with the neighbouring tissue-elements, belonging partly to the ligneous ring, partly to the pith, the structural peculiarities of which have been often mentioned in former sections, they have long been distinguished collectively as the *medullary sheath* or *medullary crown*, Corona.

In the root, the internal limit of the first annual ring has a different structure, corresponding to the conditions described on p. 473. The secondary wood here closely surrounds the original axial xylem-plates. It is quite a prevailing rule that these latter remain separated from the secondary vessels and tracheides by at least one layer of connective cells[3]. No case is known in which the secondary elements border immediately on the outermost narrow, spiral, and annular vessels of the primary plates. On the other hand, it often occurs that the inner pitted vessels (or tracheides) of the original plates stand in immediate connection with equivalent elements of the secondary wood; this has been observed in Taraxacum and Ranunculus repens (Fig. 165, p. 356).

The cells which usually border on the xylem-plates consist of the inner layer of those connective cells which were originally present in this position, while from their outer layer the cambial ring bordering on the phloem-group has been derived (pp. 351, 473). In those cases where the pitted vessels are contiguous, it still remains to be investigated whether the latter are derived directly from the above-mentioned connective cells, or from a cambial zone which, in the latter case, must originate in the innermost layer of connective cells. All the tissue-elements of the region in question usually become very thick-walled, and have relatively narrow cavities, especially in

[1] Compare Link, Philos. Bot. p. 136.—Meyen, Physiol. I. p. 361.—Treviranus, Physiol. I. 235. —Unger, Botan. Zeitg. 1847, p. 267.—Schacht, Lehrb. II. p. 62.—Sanio, Botan. Zeitg. 1863, p. 392.

[2] Compare Botan. Zeitg. 1844, p. 367.

[3] See Van Tieghem, *l. c.*

true-woody plants. The accurate distinction of the individual elements one from another therefore presents great technical difficulties; even in good transverse sections the recognition of the original xylem-plates between their thick-walled next neighbours is often very difficult, besides which the narrow vessels at their angles often seem to become indistinct owing to pressure from the surrounding tissues.

In addition to these peculiarities of the internal limit of the wood in stem and root, further peculiarities exist in the inner secondary ligneous mass itself.

In rare cases, especially in the stem of Mahonia Aquifolium, Berberis vulgaris, Pelargonium roseum, and Solanum Dulcamara, Sanio found septate fibrous cells in the first annual ring, while they are absent in the succeeding ones. And further, in the first and next-following annual rings of the stem and its branches, in many though not all Dicotyledonous woods, although the elements characteristic of the species are all present, yet their characteristic arrangement does not appear clearly till later, as it is merely indicated in the former region. The groups of vessels, and the parenchymatous zones of Hedera Helix, Quercus pedunculata, Juglans, Casuarina, &c.[1], are examples of this. The characteristic structure of a wood is therefore not always to be recognised with clearness from its inner rings. Similar phenomena, which have not at present been accurately investigated, may occur in the case of roots.

Sect. 153. The most remarkable phenomenon of this category is the change in the average size of equivalent elementary organs, as regards both their width and length, which accompanies the growth in thickness. In most woods this change takes place in such a manner that the average size increases during a series of years, and then attains a definite value which remains constant in the succeeding years. The change in question takes place in a different manner in the stem, branches, and roots of the same tree, and in their different transverse zones; in some cases it depends on a corresponding successive increase in size of the cambial cells, while in others it is independent of this.

The most complete measurements referring to this point were carried out on Pinus silvestris by Sanio[2], who determined the mean length of the tracheides, and their mean tangential breadth in the autumn wood. He thus sums up his results:—

1. In the stem and branches the tracheides everywhere increase from within outwards, throughout a number of annual rings, until they have attained a definite size, which then remains constant for the following annual rings.

2. The constant final size changes in the stem in such a manner that it constantly increases from below upwards, reaches its maximum at a definite height, and then again diminishes towards the summit.

3. The final size of the tracheides in the branches is less than in the stem, but is dependent on the latter, inasmuch as those branches which arise from the stem at a level where the tracheides are larger, themselves have larger tracheides than those which arise at a level where the constant size is less.

4. In the gnarled branches of the summit, the constant size in the outer annual ring also at first increases towards the apex, and then falls again; but here irregularities occur, which may be absent in regularly grown branches.

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[1] Sanio, Botan. Zeitg. 1863, p. 397.

[2] Pringsheim's Jahrb. VIII. p. 401, &c.

5. In the root the width of the elements first increases, then falls again, and next rises to a constant amount. An increase in length also takes place, but could not be exactly determined.

The absolute size of the elements is not the same at the same place in different individual trees, but these differences do not infringe the general rule. In order to illustrate the absolute dimensions, some of Sanio's determinations (cf. *l. c.*), taken from a main axis 110 *years old*, may here be cited.

ML. = mean length, *MBr.* = mean breadth of the tracheides, the latter determined in the autumn wood.

A. Disk 21 years old, from the summit.
B. „ 35 „ „ above the thick branches of the crown.
C. „ 72 „ „ from the shaft, 36′ above the ground.
D. „ 105 „ „ close above the ground.

The dimensions are expressed in millimetres.

A.

Annual ring.				
1	MBr.:	0·016;	ML.:	0·78
14	„	„	„	1·74
18	„	„	„	2.21
20	„	„	„	2·91
21	„	0·026	„	2·82

B.

Annual ring.				
1	MBr.:	0·016;	ML.:	0·80
15	„	„	„	2·60
17	„	„	„	2·74
18	„	„	„	2·82
19	„	„	„	2·82
20	„	„	„	2·82
22	„	„	„	2·82
35	„	0·028	„	2·78

C.

Annual ring.				
1	MBr.:	0·017;	ML.:	0·95
17	„	„	„	2·74
19	„	„	„	3·13
31	„	„	„	3·69
37	„	„	„	3·87
38	„	„	„	3·91
39	„	„	„	4·00
40	„	„	„	4·04
43	„	„	„	4·09
45	„	„	„	4·21
46	„	„	„	4·21
72	„	0·032	„	4·21.

D.

Annual ring.				
1	MBr.:	0·011;	ML.:	—
20	„	„	„	1·87
29	„	„	„	2·48
30	„	„	„	2·60
31	„	„	„	2·65
46	„	„	„	2·65
60	„	„	„	2·65
80	„	„	„	2·69
105	„	0·028	„	2·65

In the *Dicotyledonous woods* investigated[1], the conditions in question vary according to the species; some show no increase in the size of the elements in the successive rings: e. g. Mahonia Aquifolium; or only an inconsiderable one, as in Berberis vulgaris, where only the vessels in the spring wood become wider.

In the other cases investigated (Caragana arborescens, Sophora japonica, Sarothamnus scoparius, Acacia longifolia, Carpinus Betulus, Quercus pedunculata, Cornus sanguinea, Rhamnus cathartica, and Ficus elastica), an increase in length takes place from within outwards, which affects the individual forms of tissue unequally. The

[1] Sanio, Botan. Zeitg. 1863, *l. c.*—Pringsheim's Jahrb. IX. p. 52, &c.

fibres always increase in length. The cells of the bundle-parenchyma show no change. The members of vessels and the tracheides behave differently according to the kind of wood.

By way of example we may reproduce Sanio's statements regarding the mean length of the elements in a stem of Quercus pedunculata 130 years old, with very narrow annual rings. The dimensions are expressed in millimetres.

	Woody fibres.	*Tracheides.*	*Members of large vessels.*
1st Annual ring	0·42	0·39	—
2nd „	0·60	0·43	0·25
4th „	0·74	0·53	0·26
Three outermost rings	1·22	0·72	0·36.

An increase in the width, and in the thickness of the walls of the elements, accompanying the increase of the latter in length, is likewise evident in many Dicotyledonous woods, especially in the case of the large vessels of the spring-wood. Quercus pedunculata is a typical example of this. Sanio found the mean radial diameter of these vessels in the third annual ring $=0{\cdot}08^{mm}$; its definitive dimension, which is not attained before the sixth year, amounts to $0{\cdot}31-0{\cdot}33^{mm}$. As regards the change in the definitive constant length of the elements at different levels of the stem, only one investigation, on *a single* Birch-stem, exists, which may be referred to in Sanio's treatise.

The increase of the ligneous elements in length and width is, in some of the cases observed, the immediate consequence of a corresponding successive enlargement of the cambial cells; while in others this is not so. The former is the case in the Coniferæ, where both the successive enlargement of the cambial cells, and the relatively trifling increase of size, which the ligneous elements undergo after their origination, are distinct. In the Pine, for example, the tangential diameter of the winter cambial cells is more than twice as great ($0{\cdot}026^{mm}$) in a stem a hundred years old as in a shoot one year old ($0{\cdot}012^{mm}$); in a one-year-old apical shoot of the same species, on the other hand, the length of the cambial cells is $0{\cdot}87^{mm}$, that of the tracheides in the autumn-wood $1{\cdot}05^{mm}$. The other category includes, for example, Rhamnus Frangula, Cytisus Laburnum, Caragana arborescens, and probably most Leguminosæ. As far as the investigations extend the cambial cells here undergo little or no increase of size, as their distance from the pith becomes greater. The increase in size is thus due to the ligneous elements themselves, which have already been developed from the cambium; the woody fibres, which are especially affected by it, become in Cytisus Laburnum, for example, six times as long as the cells of the cambium.

Sect. 154. In many woody plants there further arise those differences of physical properties between successive zones of growth or annual rings, on which is founded the technical distinction between *sap-wood* (Splint, Alburnum, Aubier) and *duramen* or *ripe-wood* (Kern, Herz, bois parfait). The sap-wood is wood which has been completely developed from the cambium, and which possesses the anatomical characteristics above described, and the physiological properties which depend on them. It has a light whitish or yellowish wood-colour. In many trees, as for example Acer pseudoplatanus, platanoides, and Buxus, the alburnum condition

undergoes, according to Nördlinger, no change, at least as regards the outward appearance and coarser physical characteristics of the wood. These are termed alburnum trees by Nördlinger[1]. In most woods changes of the chemical[2] and physical character, and in a less degree of the structure also, take place sooner or later with the increasing age of the successive zones. These changes represent the beginning of that process of degradation which ends with decomposition, and as they proceed the wood ceases to be available for its original physiological work[3], with the exception of the purely mechanical function in the case of those woods which become harder. Externally a darker colour appears, which varies in the different kinds of wood, and may become deep black, as in the Ebony woods, dark-green as in Guaiacum wood, or red and violet as in the dye-woods of the Cæsalpiniæ, Pterocarpus, Hæmatoxylon, &c. With these changes is very often connected an increase of the specific weight and hardness, and a diminution of the contained water[4]; in a word the technical value of the wood is created or enhanced by these changes. In this case especially the terms 'ripe-wood' and 'heart-wood' are used;—the two names being applied rather arbitrarily to the particular cases, or used for successive stages.

The formation of hard and lasting duramen is however only a special case of the incipient process of degradation. The latter may also lead quickly to the opposite result. According to Nördlinger[5], if I understand him rightly, 'many soft woods, e.g. Canadian poplar, and several kinds of Willow,' have a brown heart-wood, which is not distinguished from the alburnum either by higher specific gravity, or by hardness and durability, but, on the other hand, shows a tendency to rapid decomposition, accompanied by the growth of mould. The complete disorganization of the wood, which in many cases takes place in old living trees, is an allied phenomenon which will be discussed below.

Apart from these changes, anatomical investigation does not demonstrate any alteration in the original structure and the original thickness of wall of the cells and tubes, on the formation of the heart-wood, but merely changes in the material properties of the walls, and in the contents. The membranes are infiltrated by heterogeneous organic bodies, and the latter often appear in the interior of the elements, which they fill up more or less completely, as well as in any cracks and crevices that may be present. The colours of heart-woods are those of the infiltrated substances.

Qualitatively, the latter are usually combustible organic compounds, showing extreme variety in detail, if all the cases be taken into consideration. While referring to the technical literature[6], it is here sufficient to call to mind the dyeing substances and chromogenetic bodies of the dye woods, and the infiltrations of resin in the wood of many Coniferæ, Guaiacum, &c. As regards these substances, it is by no

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[1] Technische Eigensch. d. Hölzer, p. 28, &c.

[2] Compare the summary in Hofmeister, Pflanzenzelle, p. 247, and the technical literature.

[3] Rossmässler, Tharander Jahrb. IV. p. 186 (according to Nördlinger).

[4] On these subjects, which do not concern us further, compare Nördlinger, *l. c.*, and Wiesner, Rohstoffe, cap. 13.

[5] *l. c.* p. 36.

[6] Compare the summary in Wiesner, *l. c.*

means to be asserted that in the woods in question they alone saturate the heart-wood, and may not perhaps be mixed with other bodies which have not been minutely investigated, or that differences may not prevail between the mixtures which occur in the membranes and those in the cavities. On these questions no sufficiently accurate investigations exist. In a number of Dicotyledonous woods, which do not serve as dye-woods (Ailantus, Prunus domestica, spinosa, Amygdalus communis, Zanthoxylon fraxineum, Rhamnus cathartica, Sorbus Aucuparia, Gleditschia, Periploca, &c.), bodies were found by Sanio[1] both in the interior of the vessels and in the membranes, which on their first appearance in the interior of the vessels were colourless, but afterwards came to differ from one another in their yellow or red colour, while they agreed together in their high resistance to all solvent agents. Caustic potash does not change them; Schulze's mixture at boiling-point first produces discolouration, and then solution.

It is thus quite possible that the appearance of a definite body, or of a series of substances, which are nearly related, and vary in the different kinds of wood, may be generally characteristic of the process of metacrasis which produces the duramen, and that the appearance of resins, of special colouring matters, and so on, may only be a phenomenon peculiar to particular cases, and accompanying the former changes.

In Caragana arborescens Sanio found that only air is at first contained in the vessels of the yellow heart-wood; at a somewhat later stage he found a yellow body with the properties above-stated; in the discoloured central portion, which is limited by a red ring, and even in the red ring itself this body had again disappeared. This phenomenon can afford no argument against the view that the appearance of the infiltrating substances in question is characteristic of the formation of duramen, but can only indicate that in certain cases they may undergo displacement, or further processes of rapid decomposition.

Inside the vessels and cell-lumina the infiltrating bodies of whatever kind appear at first in the form of deposits on the wall, often in two layers; here and there, where they are accumulated in large quantities, they show hemispherical prominences, projecting inwards, or sometimes form biconcave plates extending transversely through the lumen; the masses are homogeneous, rarely granular (Castanea vesca), frequently with flaws and cracks. All these phenomena point to the fact that they first appear in the fluid form, and afterwards harden. Very extensive accumulations fill the lumina completely, as for example in the Guaiacum and Ebony woods. In the vessels and crevices of the Campeche wood, greenish crystals (Hæmatoxylin?) sometimes occur[2].

It is remote from the purpose of this book to discuss the question, so difficult in the defective state of chemical knowledge on these subjects, as to the origin of the infiltrating substances, and more especially to investigate how far they are derived from the transformation of other pre-existing substances, at the same places in which they occur, to what extent they have been conveyed to these places from elsewhere, and in the latter cases what their origin is. Attention may

[1] Botan. Zeitg. 1863, p. 126.—Compare also Hartig, ibid. 1859, p. 100.

[2] Flückiger and Hanbury, Pharmacographia, p. 188.

here only be briefly called to the fact, that the anatomical conditions already adduced point to the occurrence of somewhat complicated processes, and that the expressions just used are not intended to prejudge any developmental theory whatever.

As a last stage of the changes described, and one which leads to a result opposite to the formation of heart-wood in the technical sense, a displacement of the normal membranes (extending to their complete disappearance) by masses of resin and balsam is stated to occur locally in the woods which produce these substances; in other woods, which do not form resin, a transformation into disorganised masses of mucilage and gum takes place. The wood of Pinus Strobus and Abies pectinata, which is infiltrated with balsam, dissolves away, according to Wigand [1], into a resinous mass, and as this goes on, the walls of the tracheides and cells diminish in thickness, becoming lost eventually in the structureless mass of resin. The canals, an inch in width, filled with balsam, which, according to Karsten [2], traverse the wood of species of Copaifera, and similar phenomena reported in the case of the stem of Drybalanops aromatica [3] can also, according to the data before us, scarcely arise otherwise than by partial disorganisation and solution of the ligneous elements.

The formation of cherry-gum by disorganisation of the wood of the Amygdaleæ, as described by Wigand, which no doubt belongs to a great extent to the province of pathology, starts sometimes from vessels, sometimes from groups of wood-parenchyma, or medullary spots. Comp. Wigand, *l. c.*

In addition to the organic infiltrated substances, considerable accumulations of Silicic acid occur, as found by Crüger [4] in the old wood of plants which are characterised by extensive silicification of almost all their parts, namely of the Chrysobalaneæ, Hirtella silicea, Petræa volubilis, P. arborea, and of Tectona grandis. They occur in the lumina of the cells and the vessels (the latter exclusively in Teak wood) as amorphous masses, filling up the space more or less completely. According to the published statements they are not present in the alburnum. The data before us do not allow of any decided judgment as to further differences between alburnum and duramen, as regards the incombustible constituents which they contain.

In the contents of the *cells* of the wood, both in the medullary rays and in the ligneous bundles, and also of the thyloses where they occur, a further essential change takes place on the formation of the heart-wood, in addition to those described. This consists in the permanent disappearance of those constituents which characterise the living cell, especially of the universally distributed starch, and in their replacement by air or infiltrations [5]. The disappearance of the starch from the cells coincides fairly exactly, in the cases investigated, with the appearance of the other characters of the heart-wood.

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[1] Pringsheim's Jahrb. III. p. 165.—On the other hand compare also Dippel, Botan. Zeitg. 1863, p. 256.

[2] Botan. Zeitg. 1857, p. 316.

[3] Compare Flückiger and Hanbury, Pharmacographia, p. 202.

[4] Botan. Zeitg. 1857, p. 297.

[5] Sanio, Stärkeführende Zellen, p. 19 (1858).—Id. Botan. Zeitg. 1860, p. 202.—A. Gris, Comptes Rendus, 1866, tom. 70, p. 603.

As has often been indicated in the preceding pages, the transformation or degradation of the alburnum into duramen takes place in different species of trees at a different average age, and in some gradually, in others suddenly. In the stem of Fraxinus excelsior when forty years old, and in that of the Birch when thirty-five years old, abundance of starch was found by Gris in *all* the annual layers; the former species is, according to Nördlinger, characterised by a very broad alburnum, while Betula alba is an 'alburnum tree.' In a stem of Fagus sylvatica ninety-five years old, investigated by Gris, there was abundant starch in the fifteen outermost annual rings, then a gradual decrease in its amount from these up to the thirty-fifth ring, while further inside it was wholly absent. According to Nördlinger, Quercus pedunculata has 8–13 annual layers of alburnum; in an oak-stem fifty-eight years old, Gris found that the cells ceased to contain starch somewhat suddenly at the sixteenth ring, and in one ninety-eight years old, at the twenty-first ring. Robinia Pseudacacia has 3–5 rings of alburnum, which are sharply marked off from the dark heart-wood, both by their containing starch, and by their light colour: Castanea vesca behaves in a similar way (Gris and Nördlinger). According to statements based on those coarser differences which are of technical importance, the diversity in this respect is very great.

It is equally evident from the facts already mentioned, that in the same species of tree, and even in the same individual, stem, or branch, numerous individual variations occur, within definite specific limits, according to the age and vigour of development, especially of wood-formation, and at different levels of the stem. This is the case whether the relative thickness of alburnum and duramen be determined according to the number of annual rings, or according to absolute measure. Even on different sides of the same cross-section the number of annual rings showing the properties of alburnum is often different[1].

What has been hitherto said applies to wood enclosed in the uninjured stem. It is well known that changes not unfrequently occur in the wood in consequence of injuries, and that the extent of these changes, which are similar to those characterising the formation of heart-wood, shows a definite relation to the position and extent of the wound. The processes of decomposition to which they owe their origin may often be different to those which accompany the formation of duramen[2]. On the other hand, the phenomena occurring in both cases are often so similar—as for example the conversion into resin in the Coniferæ, and the formation of black, hard wood in the Ebenaceæ—that we may suppose the same process, which usually comes on more slowly, to be accelerated or excited by injury.

e. *Individual and local deviations.*

Sect. 155. Within the limits of the typical characteristics, which have been explained in the preceding pages, the structure of the annual ring in the same species shows definite variations, according to differences, however produced, in the vigour of its development; the single feebly developed ring, or even portion of a

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[1] Compare especially the detailed statements respecting the Oak in Duhamel, Physique des Arbres, I. p. 46, &c.

[2] Compare e. g. Nördlinger, *l. c.* p. 37.

ring, of a tree which has otherwise grown vigorously, shows essentially the same character as the whole of the rings of a feebly thickened tree. This character is different in Coniferous woods, and in the Dicotyledonous woods investigated.

In the former, according to Mohl, the relative thickness of the spring-wood with wide lumina, and the autumn-wood with narrow lumina, and the more or less sudden transition from one to the other, varies quite universally, according to the thickness of the rings, the variation in the stem being, as a general rule, in the opposite direction to that in the root, subject to specific or perhaps individual modifications[1]. In the former, the outer zone of the ring, with narrow lumina and thick walls, forms a larger portion of the whole, and is the less sharply marked off from the interior the thinner the ring is. In the root it is the more developed the thicker the ring; in the feeble annual rings which are prevalent in roots, and which in the White Fir (Abies pectinata), for example, are on the average only about $0{\cdot}2^{mm}$ broad, it often consists of only 3–1 layers, and is sharply limited towards the internal zone, which has wide cavities.

In the Dicotyledonous woods investigated (Fraxinus, Fagus, Quercus pedunculata, Morus, Broussonetia, Rhus, Sophora, Gymnocladus, etc.)[2], the middle portion of the ring becomes reduced, as the thickness of the whole diminishes, in such a degree that in extreme cases the ring consists exclusively of spring-wood and the autumnal limiting layer. This condition appears most sharply in Morus, Rhus, and the Leguminosæ mentioned, where the woody fibres are confined to the middle region in well-developed rings, but wholly disappear in feeble ones. In this respect the wood of stem and root shows a general agreement, and as the annual rings, in roots which have once attained a thickness of two or three inches, are, as a rule, extremely thin ($0{\cdot}25^{mm}$ and less in thickness), it follows at once that there is a considerable difference in the general structure of the wood of stem and root, which is increased by further differences in the structure and distribution of the elements, which will be described below.

As in Coniferous woods the outer portion of the annual ring contains relatively the largest mass of lignified membranes, and consequently possesses the greatest density, strength, and hardness, while in Dicotyledonous woods, owing to the structure and distribution of their elements, this is the case with the middle parts of the ring, the lesser density and strength of the wood of the root, as compared with that of the stem, is a necessary consequence of the facts above stated. The stem-wood, however, as technically made use of, when taken from well-grown trees, for which the exceptions to be mentioned below do not hold good, diminishes in the case of the Coniferæ in density and strength as the thickness of the annual rings increases, while in Dicotyledonous woods the reverse is the case.

These rules, however, undergo a considerable modification in the case of stems, owing to local changes in the relative breadth of the autumnal wood at different levels on the stem, as Sanio[3] found in some well-grown main axes of Pinus sylvestris. In these cases the relative breadth of the autumnal wood increases in

[1] Compare von Mohl, *l. c.* p. 238.
[2] Compare von Mohl, Botan. Zeitg. 1862, *l. c.*—Sanio, ibid. 1863, p. 397.
[3] Pringsheim's Jahrb. IX. p. 115.

every annual ring, independently of its total breadth, from apex to base, so that, for example, the proportion between autumn- and spring-wood in the same three outermost annual rings amounts to 1 : 10·6 at a height of 27^m, and to 1 : 2·5 at a height of 1^m. The strength and technical usefulness of the wood at different levels on the stem is thus very unequal. According to the statements of technical authorities[1], who value the wood of the upper trunk of Dicotyledons and Conifers less than that of the lower, it may be conjectured that similar conditions to those found by Sanio in the Pine are of general occurrence in the stems of trees; yet these differences in technical usefulness might also have other causes, e.g. differences in the formation of heart-wood, or the causes might be various in the various cases. More extended investigations are still required before any general rules or laws can be laid down.

Sect. 156. The indistinctness of the limits between the annual rings, which in many woods is typical (comp. p. 503), may also occur in those with a typically sharp demarcation, as an individual phenomenon, especially where the rings are slightly developed; in cases of eccentric ring-formation this often takes place in such a way that two distinct rings on the stronger side run together into a single one on the weaker. Such an obliteration of the boundaries of rings has often been observed, in the case of Dicotyledonous and Coniferous trees, both in the wood of the stem, and more especially in that of roots[2]. Both in the cases of unilateral coalescence of otherwise distinct rings, and in those where the number of the existing complete rings is less than the known age of the wood in years, a distinction must be drawn between the partial or total suppression of the *growth in thickness* during a period of vegetation, and the suppression of the *demarcation of rings* where growth takes place. Both cases may occur, the former, for example, has been demonstrated in stunted trees[3]; when a case comes under investigation, it can, as a rule, scarcely be determined subsequently which of the two phenomena has taken place.

As already indicated, the Araucarias appear, according to the existing data and controversies[4], to have a special inclination to the individual differences in question during the occurrence of growth in thickness. Schacht denies the demarcation of the annual rings in A. brasiliensis, even in the face of Göppert's reply. Kraus, on the other hand, describes two pieces of the stem of the same species, one of which had concentric zones, but not a trace of an annual boundary, while the other had eleven annual rings, characterised by sharply defined autumnal and spring-wood. In a portion of the stem of a well-grown specimen of A. excelsa (cultivated in the open ground) I found sixteen rings, which were so sharply marked when seen with the naked eye that one is astonished to hear of its being necessary to seek them with high powers in thin sections. This is explained by the fact that every ring consists principally of thick-walled, tolerably uniform tracheides, and only contains a narrow zone of more thin-walled elements (spring-wood) at the boundary of the next inner ring. These are but little wider than the thick-walled ones, a sharp boundary between the two being as little observable as a distinct flattening of the latter. For these reasons the limit between the rings is by no

[1] Compare Nördlinger, Techn. Eigensch. d. Hölzer, p. 130.

[2] Compare T. Hartig, Forstl. Culturpfl. p. 86.—Von Mohl, Botan. Zeitg. 1862, p. 228, &c.—Kraus, Bau d. Nadelhölzer, *l. c.* p. 146.—Nördlinger, Der Holzring, p. 21.

[3] Compare R. Hartig, Botan. Zeitg. 1870, p. 527.

[4] On these compare Schacht, Göppert, Botan. Zeitg. 1862, and Kraus, *l. c.*

means conspicuous under microscopical investigation, while the middle of the thin-walled zone appears to the naked eye as a sharp line of demarcation. Possibly the same conditions may exist in the stems of A. brasiliensis, which have been the subject of controversy. A branch of the same specimen of A. excelsa, about 2^{cm} thick, with narrow rings, shows the same characteristics in some parts, while in others there is a decided flattening of the tracheides at the autumnal limit.

The question whether the formation of two successive rings in one period of vegetation occurs as an individual deviation from the rule, even in our woody plants which typically form a single ring, is essentially foreign to the present anatomical survey. It must be remarked, however, that this phenomenon is stated to occur as a rare exception, and in fact as a consequence of the interruption of the summer growth by external causes (frost, drought, attacks of insects, hailstorms [1], &c.). As regards the anatomical characteristics of these anomalous double annual rings, no other statements have been published, than that the boundary between them is usually indistinct: only in the case of shoots of Sambucus nigra, interrupted by a hailstorm in very vigorous vegetation in 1846, does Unger mention 'two distinct woody rings.'

Sect. 157. The existing investigations show that the structure of most woods remains essentially constant, within the limits defined by the preceding statements. But exceptions even to this rule occur, the most remarkable of which are afforded by the Ash (Fraxinus excelsior [2]). In a well-grown tree of this species, the annual ring, which is about $2–3^{mm}$ in breadth, shows on the inside a zone of spring-wood, consisting of slightly thickened fibres, between which wide vessels surrounded by bundle-parenchyma are inserted; then follows externally the thick middle layer, consisting of thicker-walled fibres, with scattered smaller vessels, likewise surrounded by bundle-parenchyma; finally, at the outside, there is the autumnal limiting layer, consisting of several rows of bundle-parenchyma, with small, very thick-walled vessels. In very thin annual rings, the reduction of the middle layer takes place as described above. In the case of very luxuriant young trees, grown on damp soil, with annual rings over 12^{mm} thick, V. Mohl found the fibres less thick-walled, and the vessels, especially the large ones, narrower than in moderately thick rings. Sanio found a specimen which differed conspicuously from the usual form, in having concentric zones of parenchyma, containing narrow vessels in the middle layer; in one piece only there was an annual ring similar to the usual type. Another stem, which was stunted, and at an age of fourteen years was only 15^{mm} thick, showed a strikingly feeble development, and in the thinnest rings actual suppression, of the characteristic spring layer, in contradistinction to the rule holding good for narrow annual rings, while the vessels were everywhere remarkably narrow. The mean width of the largest of the latter in one ring was $0{\cdot}07^{mm}$, that of the large vessels in V. Mohl's broad-ringed stems was $0{\cdot}17^{mm}$, while in normally grown trees it is about $0{\cdot}26^{mm}$.—Sparmannia africana, as more minutely described by Sanio, *l.c.* p. 399, shows a conspicuously different structure, even in successive transverse portions of the same stem, or on different sides of the same ring, broad bands of irregular large-celled parenchyma being sometimes present, sometimes absent.

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[1] Unger, Botan. Zeitg. 1847, p. 265.—Nördlinger, Holzring, p. 10.
[2] Von Mohl, *l.c.* p. 269.—Sanio, Botan. Zeitg. 1863, p. 398.

f. *Differences of the secondary wood in non-equivalent members of the same plant.*

Sect. 158. The ligneous body of the stem and its branches has, in the plants in question, the same structure, within the limits of deviation defined in the preceding pages. In trees, however, differences in dimensions exist, owing to the fact that not only the thickness of the annual rings, but also the size of the tissue-elements, is less in the branches than in the stem. This at least is the case according to the more accurate investigations before us, which were carried out on Coniferous trees, and are mentioned at p. 506 [1].

A far less general agreement prevails between the special structure of the ligneous body in the stem and its branches on the one hand, and in the roots of the same plant on the other. Here, on the contrary, there are two different extreme cases; plants with the wood of the root completely similar to that of the stem, and others with the opposite character; between the two extremes there are of course many intermediate cases.

The first of the two cases occurs in Gymnospermous and Dicotyledonous trees and shrubs. Although the wood of their roots is never quite similar to that of the stem in form, structure, and distribution of the tissue-elements, yet the differences only affect relative dimensions and subordinate variations of structure [2]. Differences of the former class consist, firstly, in a considerable reduction, in the case of the root, of the average thickness of the entire annual ring, which, though subject to great variations, may sink to minimal dimensions, in the White Fir, for example, to $0{\cdot}117^{mm}$, although, on the other hand, it sometimes reaches $2–3^{mm}$; in Dicotyledonous woods it may even be smaller than the average diameter of the vessels present in the annual ring, in which case the ring must have an undulating outline, widened at the vessels. Secondly, there are differences in the width and thickness of wall of equivalent portions of tissue. These affect details in the structure of the walls, and, in the case of Dicotyledonous woods, the distribution of the non-equivalent forms of tissue in the annual rings. These relations once more appear most clearly and simply in the Coniferous woods. According to V. Mohl's measurements, the tracheides of the spring-wood in the root of the White Fir are distinguished from those of the stem by this fact, that their radial diameter is on the average $\frac{1}{4}$, and their tangential diameter $\frac{1}{5}$ greater, while their length is also greater; those of the autumn-wood by their greater radial diameter and wider lumen. To this is often added a diminished absolute thickness of wall in the tracheides of the root, and, *perhaps* independently of this, a greater softness of the wood; further, the fact that the development of the thicker-walled autumn wood-cells diminishes with the thickness of the annual rings, and in very thin ones is almost suppressed. Similar relations, to be compared in V. Mohl and Schacht, *l.c.*, reappear in other Abietineæ. The differences between the wood of the root and that of the branches, which Schacht compared with it, are as regards the width of the tracheides even greater than in the case of the stem-wood, for reasons stated above. In the wood of the root in Coniferæ, the pits on the radial sides of the tracheides are often arranged in two longitudinal rows, whether the side

[1] Compare also von Mohl, Botan. Zeitg. 1862, p. 461.—Schacht, ibid. p. 409, &c.
[2] Von Mohl, Botan. Zeitg. 1862, pp. 225, 269.

be in contact with one neighbouring tracheide, or with two (as is the case where the elements form alternate rows), while in the stem the presence of a single row of pits is the rule. (Comp. p. 494).

The wood of the root in *Dicotyledonous woods* is generally also distinguished from that of the stem by its greater 'porosity' and softness. On the one hand, this character is closely related to the changes in the structure of the annual rings which accompany their decrease in thickness, as described above at p. 512. As in the woods investigated the middle strong part of the rings is reduced in the slightly developed ones to such an extent that it may even be entirely absent, and these rings thus consist principally of the wide and relatively thin-walled vessels of the spring-boundary, the distinction indicated must necessarily result. In themselves the large vessels of the wood of the root are inferior in average width to those of the stem-wood, in the case of the Ash and Oak. In the Beech, on the other hand, and in a less degree in the Birch and Aspen also, the average width of the internal vessels, even in relatively thick annual rings, is greater than in the stem. This increase in the relative extent of the total area of the cavities of the vessels is, according to V. Mohl, the only anatomical cause of the greater porosity of the wood of the root in the Beech and Aspen. Further, in other cases a more or less considerable increase in the width of tracheides and cells is found (amounting to $\frac{1}{3}$ in Berberis), and a corresponding decrease in the average thickness of their walls. Besides Berberis, this is the case in Fraxinus, Betula, and Quercus.

Sect. 159. The second of the two extreme cases distinguished within the general plan of structure, namely, an extremely *different anatomical composition of the wood of the root*, as compared with that of the stem and its branches, is of very general occurrence among herbaceous Dicotyledons, especially perennials and biennials, the roots of which store up reserve substances such as starch, inulin, &c., and apparently large quantities of water. The distinction is no doubt most strikingly marked in the fleshy tap-roots of cultivated plants, Brassica Rapa and Napus, Daucus, Raphanus, &c.; but these are only special cases of a phenomenon which is of very general occurrence. The most general anatomical character of these roots consists in the reduction of the specific woody elements as compared with the parenchyma. This is brought about in different ways:—

(1) By feeble development of the entire ligneous body lying inside the cambium as compared with—

a. The persistent parenchymatous primary outer cortex, or

b. The relatively very thick, also chiefly parenchymatous, secondary bast.

(2) By the development of a relatively small quantity of specific woody elements, i. e. vessels and fibres, in the ligneous body, which as a whole is strongly developed.

As examples of (1) *a.* the annual subsidiary roots, approaching 2^{mm} in thickness, of some Asclepiadeæ are to be mentioned. In the shrubby Asclepias curassavica the wood of these roots is more than 1^{mm} thick, cylindrical, and similar in structure to the wood of the stem. In the thick roots of the rhizome of A. Cornuti and Vincetoxicum officinale the greatest diameter of the original diarch xylem-plate is less than 0.3^{mm}; the breadth of the secondary mass of wood attached to it is only half as much; all the rest, except the slight zone of bast, is primary cortical parenchyma. The subsidiary roots of the Piperaceæ further belong to this category, as also do those mentioned at p. 355, which show no thickening of their vascular bundles, or mere indications of it.

The far more frequent case mentioned under (1) *b.*, to which we shall have to return in considering the changes of bast and cortex, occurs, for example, in the root of Taraxacum, Rubia, and Umbelliferæ. A root of Taraxacum which is now before me, 4^{mm} in thickness, has, for example, a ligneous body only about $0{\cdot}5^{mm}$ in diameter.

Lastly, case (2), which especially belongs to the present subject, occurs in its most typical form in Brassica and Raphanus. The main mass of the Radish and the Turnip is formed of the chiefly parenchymatous wood; the bast and external cortex are not more than $1-2^{mm}$ thick. Between the typical cases mentioned under (1) *b.* and (2), a number of intermediate forms occur, with but slight difference between the mass of the wood and that of the bast and external cortex, e.g. roots of the Umbelliferæ, Scorzonera hispanica, Rheum Rhaponticum, &c. But in these cases, as the relative thickness of the wood increases, the proportion of parenchyma to the specific woody elements increases in favour of the former, if it is allowable to enunciate a general rule for cases which show such great variety in detail.

In the roots in question, the tracheæ of the wood, in all known cases, are exclusively vessels, with a wall which is reticulately thickened (and then often with scalariform transverse meshes), or has bordered pits, the latter structure being not uncommonly found on the surfaces which abut on other vessels, the former on those adjoining non-equivalent tissue. Their average width is considerable; wider and much narrower ones frequently occur together. They are always immediately accompanied by rows of elongated prismatic cells with pointed or horizontal ends, which may be called fibrous cells in the sense defined above, and the nature of the contents of which still requires more accurate comparative investigation; they are further accompanied by short-celled parenchyma, which in form and position corresponds to the bundle-parenchyma. Tracheides do not seem to occur, yet this point also still needs further investigation. Between the ligneous bundles, which are thus constructed according to the general rule, medullary rays of different orders are inserted as the wood becomes more strongly developed, in a manner which likewise corresponds to the general rule. So far as is known these are always parenchymatous, and their elements are generally to be distinguished from those of the bundle-parenchyma by their form and position, and the special nature of their contents, according to the rules described above; but in the particular cases the differences may be either very clear or not distinct. Leaving out of consideration the cases marked (1) *a.* where the ligneous body is quite small, the formation of massive parenchyma is apportioned between the ligneous bundle and the medullary rays in two principal forms, between which of course there are again many intermediate cases.

(1) Narrow ligneous bundles are separated or divided up by broad parenchymatous medullary rays. They consist principally of vessels and fibrous cells, the latter being usually narrow, thick-walled, and lignified; the medullary rays are thick masses of parenchyma, their cell-walls for the most part thin and not lignified. The above-mentioned cases, with strongly developed main medullary rays, belong to this category, as Urtica, Cucurbita, Symphytum officinale, &c. Comp. p. 474, Figs. 203, 204.

(2) In most really fleshy roots the main mass of the parenchyma in the ligneous body belongs to the ligneous bundle itself. In its most internal portion, bordering

on the primary xylem-plates, the latter consists of vessels lying somewhat near together, and only separated by narrow one- or few-layered bands of usually non-lignified parenchymatous or fibrous cells. If, as is usually the case here, the main medullary rays are absent, one can scarcely speak of medullary rays at all, they are only indicated by single radial bands of parenchyma. In cases with a relatively small wood (Taraxacum, Rubia, &c. (1) *b*.) this condition is permanent. Where, on the other hand, the wood is largely developed (2), as in Rheum, Scorzonera hispanica, Pastinaca, and the swollen roots of Brassica and Raphanus[1], the formation of parenchyma in the ligneous bundle increases with the progressive growth in thickness. The bundle is principally composed of parenchymatous cells with non-lignified walls, decided longitudinal extension, and radial arrangement; and in this massive thin-walled parenchyma of the bundle lie the vessels, which form closely united groups, or are rarely quite isolated, and are accompanied by narrow, usually non-lignified fibrous cells. As seen in transverse section they form interrupted radial rows, increasing in number in the centrifugal direction, and concentric zones which are also interrupted, while in their longitudinal course they form a net with pointed meshes. The medullary rays are inserted between the parenchymatous masses of wood. Their cells are in many cases distinguished from those of the ligneous bundle by their form, which is usually radially procumbent, and by differences in their contents. This is the case in Rheum, where the procumbent cells of the numerous rays, which are only 1–3 cells in breadth and generally only 6–10 cells in height, are distinguished by containing an abundant yellow colouring matter (Chrysophanic acid) from the upright parenchymatous cells of the bundle, which chiefly contain starch; also in the cultivated root of the Parsnip, &c., where the uniseriate to triseriate cells of the medullary rays, densely filled with small starch-grains, contrast sharply with the narrower, elongated cells of the bundle, in which the starch is less abundant.

On the other hand, many of the cases referred to above, in which there is no sharp boundary between the parenchyma of the rays and bundles, belong to this category. As seen in cross-section, the rays may indeed be distinguished in their middle part by the greater radial elongation of their cells, by their general course, &c.; but they pass over quite gradually into the adjacent parenchyma of the bundle. So, for example, in Scorzonera hispanica, Raphanus, Brassica, and the fleshy swollen roots of Daucus.

The preceding short statements and examples are only intended to call attention to the most remarkable structural phenomena in the wood of fleshy roots. Reference may be made to the descriptions of officinal roots in the pharmacological literature (Wigand, Flückiger, and Berg), and especially to the representations in Berg's Atlas, for illustrations of special characteristics, which are extremely variable in different species, and of the no less varied intermediate forms between those ligneous masses which consist chiefly of parenchyma, and those which are, in various degrees, more woody, i. e. which agree more in structure with the wood of the stem. The variations in the structure of the wood, which may occur within the same species in different individuals, sometimes no doubt as an effect of external conditions, and in the same

[1] Compare Nägeli, Beitr. I. p. 25.

individual in roots of different order and thickness, are considerably greater in these cases than any similar phenomena which have been observed in the wood of the stem. The most conspicuous examples of this are once more afforded by plants which, in their wild form, have thin roots, but in many cultivated varieties are provided with fleshy swollen roots, as species of Brassica, Raphanus, Daucus, &c. In the main root of the wild Daucus Carota, the ratio of the thickness of the wood to that of the surrounding cortex (bast-layer), expressed according to the radii of the transverse section, is 5 : 3. The somewhat firm wood consists in the bundles partly of narrow fibrous cells, which are at least 8–10 times as long as broad, and pointed at both ends, and are provided with a moderately thickened membrane with small pits, and partly of rather wide vessels, arranged in radial bands, the walls of which show almost exclusively transverse bordered pits. Between the bundles there are numerous medullary rays, consisting of one or more layers of large, approximately isodiametric, parenchymatous cells. Further details, which might be mentioned, especially as regards the innermost portion of the wood, may here be passed over as non-essential. In the cultivated yellow carrot, the proportion between the radius of the cross-section of the wood and that of the surrounding, chiefly parenchymatous, cortex (bast-layer), is approximately as 1 : 7. The vessels, at least in the great majority of cases, are reticulated, with transverse meshes, fibrous cells are wholly absent, and are replaced by wide, thin-walled, parenchymatous cells, which abut on one another with horizontal surfaces, and are on the average twice as long as they are broad. Although indications of medullary rays may be recognised, they are not sharply marked off from the parenchyma of the bundles.

It seems to me remote from the purpose of this book to give a synopsis of all the woods investigated, which might serve as a key to their identification. Some assistance towards the latter object may be obtained from the preceding pages. Reference may further be made to the literature cited, especially that of Pharmacology; e. g. to Wiesner's Rohstoffe des Pflanzenreichs, Hartig's Forstl. Culturpflanzen, and his treatise, Zur vergl. Anat. der Holzpflanzen, Bot. Ztg. 1859, p. 93, and more especially to Sanio, Ueber die Zusammensetzung des Holzkörper's, &c., Bot. Ztg. 1863, p. 401. Joseph Möller's copious 'Beiträge zur vergleichenden Anatomie des Holzes,' Vienna, 1876, could not be made use of for the present work.

III. The Bast[1].

Sect. 160. The cambial ring of Dicotyledons and Gymnosperms with normal growth produces on its outer side the secondary layers of bast; these are added to the original bast-zone of the stem, which is represented by the phloem-portions of the vascular bundles. A similar process goes on in connection with the primary phloem-groups of the root, in the manner described above. The secondary zones are directly continuous with the original ones, and form, together with the latter, the entire *zone or mass of bast*. Its external limit is formed by that of the primary phloem-groups and of those portions of the medullary rays which lie between them. By means especially

[1] [Compare Möller, Anatomie der Baumrinden, Berlin, 1882.]

of the former, it is sharply marked off from the non-equivalent tissues of the external cortex, more especially in those cases most frequent in stems, where the original groups of phloem are supported or enclosed on the outside by sclerenchyma. Nägeli[1] has called this external limiting zone of the bast-layer the *cortical sheath*, a term corresponding to that of medullary sheath, used for the internal boundary of the wood.

The original structure of this limiting zone is evident from the descriptions given in preceding paragraphs; the structure of the bast as a whole depends partly upon the former, partly upon that of the secondary increment of growth to be described here. A further modification, however, results from the fact that the structure of the bast must undergo a constant change, so long as the volume of the body enclosed by it is increased by means of the activity of the cambium; for each zone thus undergoes, after its first formation, a constantly increasing extension in the direction of its surface, by which it must be in some way or other affected. So long as growth in thickness goes on, a constant transition must of necessity take place between the original conditions and those which have been modified by the peripheral extension, and in fact the successive stages of change must always come under observation in every mass of bast which is regarded as a connected whole. This fact must always be borne in mind. For purposes of description, however, it is necessary to separate the initial structure from the changes due to peripheral extension. The former will be immediately considered here, the latter in the next chapter.

The differentiation of the bast (Sect. 135) is similar to that of the wood, in so far as it consists of principal and partial strands of various degrees, which are separated from one another, or divided up by the large and small medullary rays (shortly termed *bast-rays*). The equivalent rays and strands of wood and bast correspond, and fit on to one another in the cambial zone. The original form and size of the medullary rays, and the consequent course of the strands, are the same as in the adjoining wood.

Sect. 161. Among the *forms of tissue, sieve-tubes* and *parenchyma* are characteristic, without exception, of the secondary bast of Dicotyledons and Gymnosperms with normal growth. They are, at least very frequently, accompanied by *sacs containing crystals* (comp. p. 141); further, by sclerenchymatous elements, and especially by elongated fibrous cells, the *bast-fibres*; not uncommonly also by short sclerenchyma, *stone-sclerenchyma* (*stone-cells*); while, finally, *laticiferous tubes* and *secretory reservoirs* characterise the bast of certain species or families. As has already been partly shown by the descriptions of the forms of tissue given in former chapters, especially Chap. V., all these elements in the bast, with the obvious exception of the sclerenchyma, possess delicate, non-lignified, soft walls. Nägeli has accordingly introduced the collective term *soft bast* for all those portions of the bast which are not sclerenchymatous. In most cases the elements of the soft bast are originally narrow, and continue to resemble the cells of the cambium, from which they are derived; they are often difficult to distinguish from the cambium, and from one another, especially as seen in transverse section. For this reason, but to a much greater extent owing to the fact that the softness of the tissues makes it somewhat difficult to obtain good preparations, the structure of the bast, and its distinction from

[1] Dickenwachsthum, &c., d. Sapindaceen, p. 13.

the cambium, remained for a long time extremely obscure, and the accurate representations given by Th. Hartig as early as 1837 failed to be understood, until Mohl, in 1855[1], brought them into deserved honour. For the same reasons later investigations often leave much to be desired, and the special anatomy of the bast is but insufficiently treated of by most authors.

Sect. 162. The main fundamental mass of the *medullary rays* always consists of *parenchyma*. The form and arrangement of its cells are identical with, or very similar to those of the adjacent wood. It likewise occurs in the *strands* as a constant constituent, and, like the parenchyma of the wood, it is usually derived from single or repeated transverse divisions of the tissue-mother-cells, in those portions of the cambium which correspond to the strands, and its original arrangement agrees

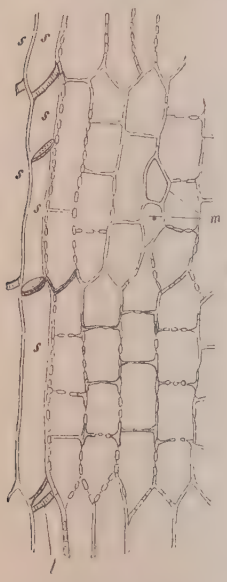


Fig. 210.

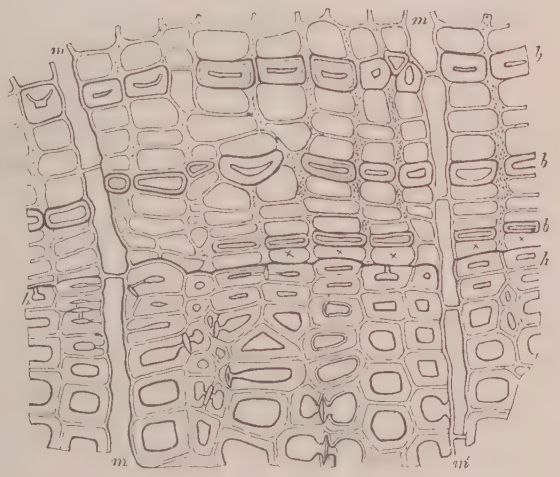


Fig. 211.

Fig. 210.—Cytisus Laburnum, tangential longitudinal section through the innermost layer of bast of the same branch as Fig. 198, under the same magnifying power as the latter; *s* members of sieve-tubes, *t* a sieve-plate lying deeper than the surface of section, *m* small medullary ray, two cells in height. The remaining elements are cells of the bast-parenchyma, the origin of which from the transverse division of cambial cells becomes clear on comparison with Fig. 198.

Fig. 211.—Juniperus communis, small stem. Transverse section through the autumnal wood, bast, and cambium, during the winter's rest (end of September); *h—h* external rows of the autumnal wood, *b*, *b* series of bast-fibres. At *x* there is only one cambial cell between *h* and *b*; *m—m* medullary rays.

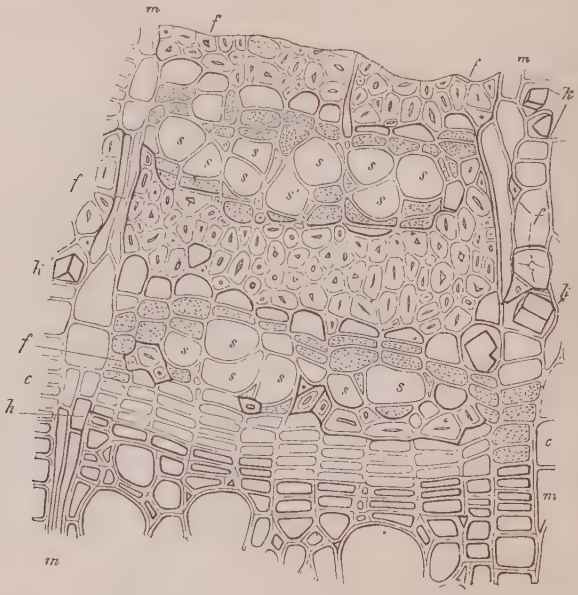
with this mode of development (Fig. 210, comp. also Fig. 198, p. 465); more rarely it arises without transverse division, from longitudinal division only of the tissue-mother-cells, and then corresponds to the intermediate cells of the wood.

The *Sieve-tubes* (Chap. V.) are constant, specific constituents of the strands in the normal soft bast of Dicotyledons. They are always accompanied by parenchyma, and in most woody plants are in general so arranged that the sieve-tubes form single, biseriate, or pluriseriate, tangential rows, which may be interrupted by parenchyma, and alternate with tangential rows of the same. The original radial

[1] Compare note on p. 172.

arrangement of the secondary elements often continues to be maintained here, or is at least recognisable; hence, in every radial row derived from the cambium, one or more sieve-tubes always alternate more or less regularly with parenchyma.

This arrangement appears with quite diagrammatic regularity in the bast of the Cupressineæ and many Taxineæ[1]. The transverse section of the bast (Fig. 211) here shows regular rows, both in the radial and tangential direction. Every fourth tangential row consists of fibres; of the three which lie between two fibrous rows, the middle one is parenchymatous, while the outer and inner each form an interrupted layer of sieve-tubes. The parenchymatous cells are approximately similar in width to the sieve-tubes (Juniperus communis), or are wider (e.g. Thuja occidentalis). In the stem of species of Pinus (P. Strobus, nigricans, silvestris), and also of Abies pectinata, irregular tangential rows of wide parenchymatous cells alternate with


m
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In the bast of Dicotyledonous woody plants, the arrangement of the two kinds of tissue, so far as can be decided from the existing data, is less regular than in the Coniferous woods first mentioned, owing to the fact that the tangential series of the one form of tissue are sometimes single, sometimes double or multiple, and are interrupted by interpolated elements of the other form; while the average width of the adjoining tissue-elements of the two kinds not uncommonly shows considerable differences, which are usually in favour of the sieve-tubes, e. g. Tilia and Vitis; more rarely in favour of the parenchymatous cells. The narrower parenchymatous cells which accompany the sieve-tubes here show the same arrangement and the same characteristics as the *cambiform cells* described at p. 324, in the case of the primary vascular bundles; they should therefore be designated by the same name. They appear in transverse section as narrow, three or four-cornered meshes contiguous with the tubes, sometimes on one side of them, sometimes on more than one, but never (?) on all sides, each side, however, never having more than one (Fig. 212).

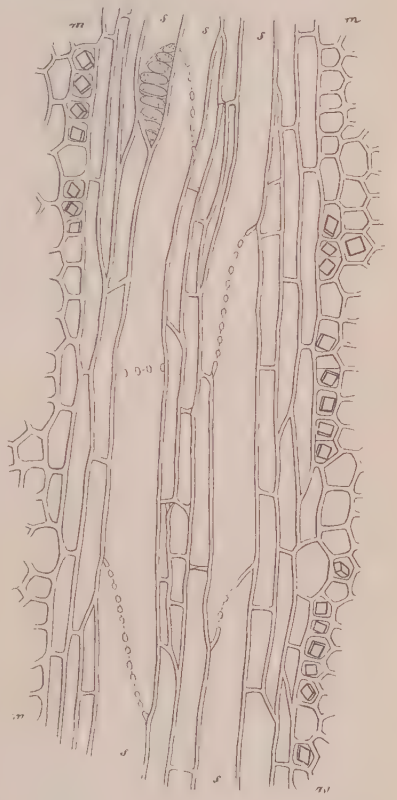

FIG. 213.—Vitis vinifera; bast of a branch several years old, 1 cm. in thickness, in summer (beginning of July). Tangential section (145). *s, s* sieve-tubes, the inclined scalariform terminal surfaces, and one which is horizontal, being cut through longitudinally, with the exception of one at the upper edge, which is seen obliquely in superficial view. *m, m* medullary rays; on the boundary between these and the strand of sieve-tubes are sacs containing crystals.

Traced longitudinally (Fig. 213) they form, in most cases at any rate, series, each member of which is many times shorter than the adjoining member of the sieve-tube, and is derived from the transverse division of the tissue mother-cell. In Tilia I rarely found them equal in length to the members of sieve-tubes. The frequency of the narrow cambiform cells seems to be very unequal in the different particular cases; for example, I find few of them in Pyrus and Spiræa ulmifolia, while they are numerous in Tilia. More accurate details are to be expected from further investigations.

In spite of the irregularities described, the radial and tangential seriation of the elements continues to be maintained in many cases in its principal outlines, and each tangential row contains for the most part either sieve-tubes or parenchyma, as is especially shown by longitudinal sections which follow its course. The most various plants, e.g. besides those mentioned, Populus, Salix, Punica, Ficus, Sambucus, Fagus (Mohl), Æsculus and Ribes, show the greatest agreement in *this* respect, although great differences occur between them in the average size of the elements and the special form of

the sieve-tubes (comp. p. 173). It may here not be superfluous to add, that, so far as my experience extends, the same statement also applies essentially to the common officinal barks, and that it is only the dried condition in which they usually come under observation which has hitherto, to some extent, impeded the clear recognition of the actual conditions.

The elements of the soft bast in woody plants of the families Apocyneæ (Nerium Oleander), Asclepiadeæ (Asclepias curassavica), Convolvulaceæ (Convolvulus Cneorum), and Campanulaceæ (Campanula Vidalii), are less regularly arranged than in the cases hitherto described, and this is no doubt also the case in the Cichoriaceæ, and in the plants mentioned at p. 324 (2), which are characterised by very small sieve-tubes in the primary bundles. Between relatively wide parenchymatous cells, which in some degree maintain the serial arrangement, groups of narrow elements are found in these instances, which, as seen in cross-section, show very various, triangular, or polygonal forms, and have apparently arisen from repeated longitudinal divisions taking place in every direction in the original mother-cells of the tissue. The narrow elements which are thus grouped are the sieve-tubes and cambiform cells; in the Cichoriaceæ, Campanula, and Lobelia, the laticiferous tubes also occur in connection with the groups of narrow elements.

The arrangement of the elements of the bundle in the soft-bast, as just described, prevails both in the stems and roots of woody plants, so far as the existing investigations extend.

There have been few minute investigations on the stems of herbaceous plants, but, according to the existing observations, they are not essentially different from woody plants with reference to the conditions here in question.

Those roots which consist chiefly of parenchyma, with a very thick secondary bast, as described above at p. 516, show in the latter a distribution of the sieve-tubes which is similar to that of the vessels in the massive parenchymatous wood of the root. A strand of bast corresponds to every ligneous strand, and the former contains relatively small groups of narrow sieve-tubes, accompanied by narrow elongated cells, and enclosed in a mass of large-celled parenchyma.

The more special distribution, relative amount, and form of the tissues under consideration is very various, according to the particular case, and often even in closely related plants. In most cases the bundles, as seen in cross-section, form relatively narrow radial bands, lying in the same straight line with the ligneous strands, between rays of wide-celled parenchyma, which essentially, though not always quite exactly, form the continuation of those of the wood. The strands consist of narrow, elongated cells, which may even be pointed like a spindle (the latter, e. g. in the wild form of Daucus Carota), and of sieve-tubes lying between them, which are always scantily developed, and are likewise narrow. The individual radial bands, like the ligneous strands, are either continuous, or are more or less interrupted by interpolated large-celled parenchyma. Examples of this arrangement are afforded by many roots of Umbelliferæ, Scorzonera hispanica, Cichorium, Argemone, &c.

In the roots of Rhubarb (Rheum undulatum and Rhaponticum) essentially the same distribution reappears, but is modified by the forms and relative numbers of the histological elements under consideration. The uniseriate, procumbent, parenchymatous rays of the wood are continued without interruption through the zone of bast. The strands separated by them consist, as regards much the greater portion of their mass, of large, upright, parenchymatous cells, filled with starch, and between these lie the

narrow sieve-tubes, which are very isolated, and therefore easily overlooked, and are accompanied by narrow, elongated cells.

Finally, an arrangement deviating further from the usual rule is represented by the bast of the roots of Taraxacum. Narrow, concentric, annular zones containing the tubes, here alternate regularly with similarly arranged, broad zones of large-celled parenchyma, which are on the average about sixteen layers of cells in thickness. The zones containing the tubes consist of narrow cells, numerous milk-tubes, and scanty sieve-tubes; the large-celled zones consist of thin-walled cells, which are placed in very regular radial and vertical rows, corresponding to the original cambial form and arrangement. At numerous points the radial series of these elements pass through the zones containing the tubes, so as to interrupt them, without however consisting of special ray-parenchyma distinct in form from that of the annular zone. The roots of Chelidonium and Papaver are intermediate in structure between those of Taraxacum, and of the first category.

Sect. 163. In plants which have laticiferous tubes (p. 186), the non-articulated ones may be absent from the secondary bast; at least I did not find them in it in Vinca, Asclepias curassavica, and the Euphorbias; in most cases they are present, and as regards the articulated tubes especially, this is always the case so far as investigation extends; they are then characteristic companions or representatives of the sieve-tubes. The large non-articulated tubes in Ficus, Maclura, and Morus follow singly the lines of sieve-tubes. The articulated, usually reticulate tubes form groups together with the sieve-tubes, which anastomose, both within each individual strand of bast, and with those of neighbouring strands, by means of connecting branches. In the bast of the Papayaceæ the net of milk-tubes has a relatively scanty development, at least in comparison to its complexity in the wood. In the other plants belonging to this category the milk-tubes are always relatively very numerous, as is especially conspicuous in the shrubby stems (Sonchus pinnatus and Campanula Vidalii), and in the roots of Cichoriaceæ, Campanulaceæ, and Papaveraceæ: as their number increases the sieve-tubes become proportionately reduced. In the strands of bast of the roots of Cichoriaceæ (Lactuca virosa, Taraxacum) only scanty, narrow sieve-tubes are present, as has already been mentioned above; in the secondary bast of the root of Platycodon grandiflorus, I did not find the latter at all, though I do not wish to assert that they are entirely absent. This mutual representation appears in the most striking manner in the bast of the roots of Papaveraceæ: Papaver Rhœas and Argemone mexicana have only very isolated sieve-tubes side by side with the highly developed net of laticiferous tubes; in Chelidonium majus the former are more numerous, although the milk-tubes predominate; Glaucium luteum has no milk-tubes, but, on the other hand, has large groups of sieve-tubes.

Sect. 164. The occurrence of protogenetic *secretory passages* in the soft-bast has already been to some extent noticed in anticipation in Chapter XIII. They only occur in those plants and parts of plants which also possess them in the primary tissues, and by no means in all even of those. Their position appears to be always within the bundles, not in the medullary rays.

Among the Dicotyledonous families in question their occurrence in the secondary bast of stem and root in the Terebinthaceæ, Burseraceæ, and Clusiaceæ has already been mentioned above. So far as is known they are present in the

same regions in all Umbelliferæ, and in the Araliaceæ; where the bast is strongly developed they form, as seen in transverse section, interrupted radial and concentric series, differing in arrangement according to the species [1].

In the secondary bast of the stem and branches of Pittosporum Tobira, the passages appear relatively late; Van Tieghem found four concentric rows in a branch 10mm thick. They were not found in the secondary bast of the root of this plant.

Among the Compositæ which contain passages, some also have them in the secondary bast, e. g. Helianthus and Centaurea atropurpurea; in Inula Helenium the bast of the root contains wide passages, which are closed blindly, so far as is known, at both ends, and coated by a delicate epithelium: they resemble those in the secondary wood. Other Compositæ have no passages in the region mentioned, but, on the other hand, have scattered sacs, filled with secretions, in the parenchyma of the rays, e. g. Echinops and Tagetes patula (comp. p. 203).

The Coniferæ, which have such great numbers of protogenetic resin-passages in their other tissues, do not form them in the secondary bast, except in a few cases. The exceptions include, firstly, the blind ends of the horizontal passages in the medullary rays of the Abietineæ mentioned on p. 490, which extend into the zone of bast. According to Van Tieghem, longitudinal passages occur in the secondary bast of Araucaria Cookii and brasiliensis, and of Widdringtonia cupressoides, which were mentioned on p. 443. The spaces filled with resin which occur in other Coniferæ are subsequent, hysterogenetic products of disorganisation, which will be discussed in Sect. 173.

Secretory sacs, other than those containing crystals, appear in the soft bast in the plants mentioned in Sects. 33–35, and are sometimes scattered without any perceptible regularity, while they sometimes have a definite arrangement, also stated in the paragraphs mentioned.

Sect. 165. The *sclerenchymatous fibres* of the bast, *bast-fibres*, or according to the older terminology 'bast-cells' in the strictest sense, have the form and structure generally described in Chap. II. With reference to the latter, it may further be mentioned that the lamella which forms their boundary, whether towards elements of the soft-bast, or towards one another, is in these cases especially often an unlignified membrane of cellulose, which surrounds the more or less lignified, thick membrane of the fibre as a distinct sheath [2]. Comp. Figs. 211, 212.

The bast-fibres are entirely absent in the bast of many plants; both in its secondary portion, and at the outer boundary of the primary phloem. This is the case in the stems and branches of Ribes, Viburnum Lantana [3], Pittosporum Tobira, undulatifolium, Citriobatus multiflorus, Porlieria, Centradenia grandifolia, and Berberis vulgaris, and in the roots of many herbaceous Dicotyledons. Thus they do not universally form an essential constituent of the bast. In the cases where they are present, which certainly form the majority, they occur—

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[1] Compare the figures of roots of Umbelliferæ in Wigand, Pharmacognosie, and Berg, Atlas, Taf. 8, 9, 14, 22.

[2] See Graf z. Solms-Lambach, Bot, Zeitg. 1871, p. 516, &c.

[3] Hanstein, Baumrinde, p. 17.

(1) Only at the outer limit of the primary bundles, surrounding their phloem-portions (comp. p. 422), and not in the products of secondary growth. This is the case in the stem and branches of Fagus, Betula, Alnus, Platanus, Viscum, Menispermum, Viburnum Opulus, Convolvulus Cneorum, Nerium, Cornus, Punica, Camellia japonica, Drimys Winteri, Ephedra distachya, Abietineæ[1], &c.

(2) Both at the outer limit above-mentioned, and also in the interior of the secondary bast. This latter condition is no doubt the most frequent, especially among woody plants. With reference to the relative amount and distribution of the fibres, it presents very various modifications.

In the medullary rays fibres are rarely present, e.g. isolated ones in Tilia, comp. Fig. 212. The principal forms of their distribution in the bundles are the following :—

(*a*) Concentric layers or rows of fibres alternate regularly with similar layers of soft bast. The layers of both kinds in neighbouring bundles fit approximately, though not always quite exactly, one on another, so that they form annular zones, extending round the whole stem, and interrupted by the medullary rays.

This phenomenon occurs with especial regularity, as already mentioned at p. 522, in the Cupressineæ and many Taxineæ, where every fourth secondary tangential row of cells becomes a uniseriate zone of fibres, which separates two triseriate zones of soft bast from one another. Comp. Fig. 211.

Among the Dicotyledons no such strict regularity exists. The fibrous layers always consist, on the average, of two or more tangential rows, and the number of these rows changes in the same individual, both in the successive annular zones and within each individual portion of the bundle; as follows from these facts, the thickness of the zones of soft bast is also unequal. The conditions in question are also extremely various, according to the species. In the case of many species, however, a regular alternation of concentric zones of fibres and soft bast, of definite average breadth, takes place within the limits of deviation indicated, the original radial and tangential seriation of the fibres of each portion of the bundle being sometimes maintained, as in Vitis, Spiræa ulmifolia, Pterocarya caucasica, and species of Acer, though in most cases their position as seen in transverse section becomes irregular, owing to the displacements due to longitudinal extension (p. 470): Tilia, Cheirostemon, Sparmannia, Malvaceæ, Medinilla, species of Salix, Ladenbergia globosa[2], Vasconcella monoica, Guaiacum, and Clematis Vitalba; comp. Figs. 212 and 214.

(*b*) Concentric zones of fibres, alternating with soft bast, may still be distinguished generally, and in places are even regularly arranged; on the whole, however, they are irregular, as they are both interrupted in each bundle by elements of the soft bast, and are also unequal in number and dissimilar in arrangement in neighbouring bundles. This condition, with numerous variations according to species and individuals, and in the average number and breadth of the successive zones, is characteristic of the bast of very many woody Dicotyledonous plants,

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[1] Compare Hartig. Forstl. Culturpfl. pp. 13, 212, 326, &c.—Hanstein, *l.c.* p. 21.—Schacht, Der Baum, p. 381.—Von Mohl, *l.c.* p. 891.

[2] Berg, Atlas, Taf. 29.

e. g. Quercus, Corylus, Carpinus, Pyrus, Juglans regia, Sambucus nigra[1], Daphne Mezereum, Rhamnus Frangula, Simaruba officinalis[2], Ulmus[3], Glycine sinensis, Quillaja, Olea europæa, and Populus pyramidalis. In these cases the fibres of each group are seldom radially arranged; their arrangement as seen in cross-section is usually irregular.

(*c*) The bast of numerous other Dicotyledons contains fibres scattered throughout the soft bast, singly or in small groups, as seen in cross-section; traced

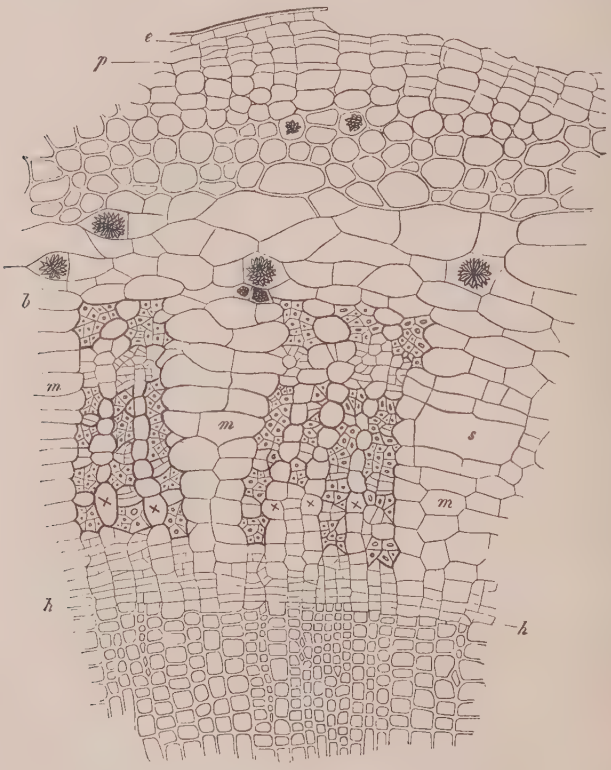

FIG. 214.—Sparmannia Africana; branch, transverse section (80). Below *h*—*h* is wood; above *h*—*h* is first the cambial zone, then higher up and towards the outside is the layer of bast, the outer limit of which lies at *b*; *m* larger medullary rays; the single radial rows marked × × are the smaller ones. Alternating with the medullary rays are narrow strands of bast, consisting of alternate groups of fibres and of soft bast with narrow cavities. On the external boundary of the bast are sacs or cells with stellate crystals. *e* remains of the epidermis; *p* periderm; *s* remains of a sac containing mucilage, after the mucilage has been washed out.

longitudinally they are also isolated, or form narrow strands, anastomosing with others at an acute angle; sometimes they are distributed over the tranverse section in large numbers, as in the external zone of bast of Ladenbergia magnifolia, and in the bast of most Cinchonas[4], also in Ficus elastica, Morus, and Celtis[5];

[1] Von Mohl, *l. c.* p. 879.
[2] Berg, Atlas, Taf. 28, &c.
[3] Hartig, *l. c.* p. 466.
[4] Compare Berg, Atlas, Taf. 29-35.
[5] Hartig, Forstl. Culturpfl. p. 450.

sometimes they occur in relatively very small quantities, as in the inner zone of bast of the Ladenbergia last-mentioned, and in the officinal barks of Cinnamomum, Croton Eluteria[1], Larix europæa[2], and Mahonia Aquifolium.

As the fibres are included in the general serial arrangement of the bast, it follows that the more closely they stand, the more distinct in this case also are the interrupted, radial, and concentric zones which they form, as e. g. in Cinchona macrocalyx, figured by Berg, *l. c.*, Taf. 35, and very beautifully in Laurus Sassafras. In general, numerous intermediate cases occur between the forms of distribution enumerated here and under *b*, as was to be expected beforehand. In this respect the cortices of Cinchonaceæ present an instructive series of gradations. Ulmus also deserves to be again mentioned here.

The appearance of *short sclerenchymatous elements* (*stone-elements*) in the bast will be considered in the next chapter, in order to avoid repetitions.

Sect. 166. *Sacs containing crystals* are often a characteristic, sometimes even a predominant, constituent of the secondary bast; their occurrence however is as far from being universal as is that of the fibres. They lie both in the medullary rays and in the bundles, in the latter usually forming longitudinal rows with short articulations; each of these rows is derived from a single mother-cell, and may often be isolated as a connected series; they were termed septate sacs at p 139 (comp. Fig. 213). Guaiacum and Quillaia have already been mentioned above as forming at least partial exceptions to this mode of arrangement; it may be left an open question how far similar, i. e. short, isolated sacs, may further occur elsewhere in the bundles, or not; no minute investigations on this point have been published, and the statements as to the distribution of crystals, which are chiefly based on transverse sections, do not admit of any decision on the question. The form of the crystals is either klinorrhombic, or that of clusters, raphides, or granules; one or more definite forms are characteristic of each particular case (comp. p. 142, and Sanio, *l. c.*).

With reference to the presence or absence of the crystal-containing sacs, and their distribution in the former case, the following phenomena have been observed, which however, at least so far as my own observations are concerned, still require re-investigation.

I indicate those forms of the crystals, which have been *chiefly* observed in transverse sections, in parentheses (K = klinorrhombic, C = clusters, R = raphides).

1. Crystals are absent from the secondary bast: Drimys Winteri, Fraxinus, Syringa, Jasminum fruticans, Mahonia Aquifolium (?), Laurus Sassafras, Cinnamomum aromaticum (Cinnamon Cassia), Clematis Vitalba, Atragene, Aristolochia Sipho (?), Camellia japonica, Sorbus Aria, and, according to Hartig (Forstl. Culturpfl.), also Cornus. As regards the sacs containing the crystals, the Cupressineæ, Taxineæ, and other Coniferæ, and Ephedra, are also to be included in this series, as in these the Calcium oxalate is not deposited in the interior of sacs or cells, but is intercalated in the membranes. In most of the plants just mentioned I find that crystals are also absent from the primary cortex.

2. Crystals are contained in the secondary bast (and then usually or always also in the primary bast, and in the external cortex). In these cases they occur—

[1] Berg, *l. c.* 36, 37.

[2] Hartig, Forstl. Culturpfl. p. 13.

(*a*) Both in the medullary rays and in the bundles: Nerium Oleander (K), Simaruba officinalis (K), Canella (C), Platanus, Cinnamomum zeylanicum and its allies (small raphides, chiefly in the medullary rays), Juglans regia (C, Sanio), Acer platanoides (K), Sparmannia Africana (C), Carpinus Betulus, and Corylus Avellana (K, C, Sanio).

(*b*) In the bundles, exclusively, or to much the greater extent: species of Salix (C, K), Pyrus communis (K), Punica (C), Ribes (C), Guaiacum (K), Galipea officinalis (R, K), Maclura aurantiaca (K), Ulmus (K), Quillaia (K), Æsculus (K), Rhamnus Frangula (C), Quercus pedunculata (K, C), Betula verrucosa, Alnus glutinosa (K, C, and granules, Sanio), and Porlieria hygrometrica (K).

(*c*) Exclusively, or to much the greater extent, in the medullary rays, and when the latter are of considerable breadth, most abundantly at their boundary towards the bundles: Vitis (K, R), Tilia (K, C), Cheirostemon (C), Olea europæa (very small R), Ficus elastica (K), Croton Eluteria (C), Pistacia Lentiscus (C), Prunus Padus (C, K), P. avium (C), Kerria japonica (C), Berberis vulgaris (scanty K according to Sanio), Lonicera tatarica (Sanio), and Sambucus nigra (granules, Sanio).

The crystal-containing sacs, especially those which are septate and contain klinorrhombic crystals, appear in many cases in company with the bast-fibres, as pointed out by Schacht[1]; e. g. species of Acer, Pomaceæ, Ulmus, Quercus, Salix, &c.[2] Clusters often occur exclusively and in large quantities where fibres are absent, e. g. Punica and Ribes; though the entire absence of the tissue last-mentioned may also occur in connection with the entire absence of crystals, e. g. Drimys Winteri.

No constant relation however exists between the presence or absence of the two forms of tissue mentioned, or between any definite form of tissue and of the crystals, as is evident from the facts stated. Thus klinorrhombic crystals are especially often present in abundance where fibres are absent in the secondary bast, e. g. Porlieria and Nerium; while, on the other hand, the klinorrhombic companions of the fibrous bundles are absent in Juglans regia and many other cases. And further, where the fibrous bundles are accompanied by crystals, the occurrence of the same or another form of crystal in the soft bast is by no means excluded.

In the soft bast the rows of sacs containing crystals have in most cases an irregular, scattered position in the transverse section. On the other hand, they are often arranged in concentric zones, which alternate regularly with zones destitute of crystals. This is the case in Punica Granatum, where the whole bast appears regularly striated in transverse section, owing to the fact that uniseriate zones, consisting almost exclusively of crystal-sacs, alternate with zones each consisting of a few rows of cells, which are destitute of crystals; these zones are interrupted by numerous uniseriate medullary rays, which are also destitute of crystals (comp. Fig. 215, and the beautiful figure in Berg, Atlas, Taf. 40, which however is not quite correct in the details). In species of Ribes also, the bundles, which are separated by broad medullary rays without crystals, consist of multiseriate zones of soft bast, likewise destitute of crystals, which alternate regularly with usually uniseriate uninterrupted zones, containing clustered crystals[3].

Sect. 167. As regards the changes of structure corresponding to the successive

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[1] Der Baum, 1 Aufl. pp. 228 and 238. [2] Compare Sanio, *l. c.*

[3] Compare Hanstein, Baumrinde, Figs. 15–17.

zones of secondary growth, to the non-equivalent members, and to individual differences, there is far less to be said in the case of the bast than in that of the wood, partly, no doubt, owing to the really greater simplicity of the phenomena, partly because it is better to pass over a number of the known changes and to discuss them in the next chapter, and lastly, in no small degree, because, for reasons already stated above, there is still an absence of any very minute or extended investigations on the subject.

In woods, the ligneous elements and cambial cells of which increase successively for a time in size (p. 505), the same is generally the case in the bast, as would be expected beforehand, on account of the enlargement of the cambial cells. This is evident on observation in the case of numerous Coniferæ and Dicotyledonous woods, e. g. Tilia, Fagus, and Nerium, also Vitis and Cobæa. It is obvious that only those internal zones must here be taken into consideration, which have not as yet undergone any subsequent dilatation. No very accurate investigations have been published on the degree and the persistency of the general increase in size, nor on the possibly unequal participation of the particular forms of tissue in these changes.

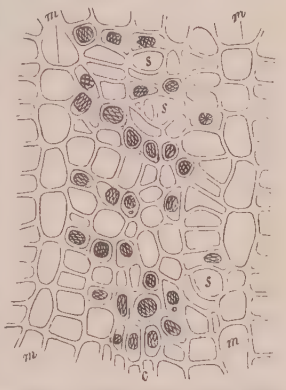

FIG. 215.—Punica Granatum (220); transverse section through the inner part of the bast of a branch six years old. *c* side towards the cambium; *m*, *m* two medullary rays; between the latter is a strand of bast; *s*, *s* sieve-tubes. It is uncertain which of the other cavities belong to elements of the latter kind. Between the empty cavities of the elements of the soft bast are transverse zones of crystal-containing sacs; the clusters contained in them are only indicated by shading.

Between stem and branches differences in the size of the elements appear to exist similar to those in the wood, but these also have not yet been more closely investigated. In the roots of trees and shrubs, so far as the investigations extend, the special structure of the bast is very similar to that in the stem of the same plant, e. g. Vitis, Sambucus, Tilia, and Punica. Wherein the differences, which no doubt occur, consist, cannot be stated at present. It has been repeatedly mentioned above (pp. 516 and 524) that a different relation exists between the foliage stems of herbaceous plants, and the roots which belong to them, especially when the latter are fleshy.

The thickness of the secondary zone of bast added in a definite space of time is very variable, both in its relation to the simultaneous growth of the wood, and according to absolute measure, whether in different species and individuals, or in non-equivalent members of the same plant. In both relations the extreme cases are represented on the one hand by the fleshy roots, consisting chiefly of bast (p. 516), and on the other by the woody stems of trees and shrubs.

Especially in trees with a persistent cortex, which is not thrown off by the formation of bark (Sect. 177), as, for example, the Fir and Beech, the difference of thickness between wood and bast is, as is well known, very considerable, and the absolute thickness of the latter small. In the common Beech with smooth bark (Fagus silvatica) the entire bast-zone in a stem 100 years old is, according to Hartig[1], scarcely more than 1^{mm} thick. Woody plants which periodically throw off their

[1] Forstl. Culturpfl. p. 212.

cortex by the formation of bark show a more vigorous production of bast, corresponding to the activity of this process. This phenomenon appears as an instructive individual variation in those stems of Fagus silvatica occasionally occurring which are called Stone-beeches, and are conspicuous from their thick, furrowed bark. The new production of bast no doubt takes place most abundantly in those stems, which, like the vine, annually renew their entire bast-zone, and throw off that of the previous year.

It is remote from the purpose of the present description to enter into the causal relations of these phenomena.

Generally valid anatomical characters of the boundary between successive zones, corresponding to the annual rings of the wood, may perhaps still be discovered in the case of the bast, but cannot be determined from the existing data. Even in those cases where regularly alternating concentric zones of non-equivalent tissue appear in the bast, especially fibrous zones alternating with soft bast, their number varies according to the year, the age, and the individual, and a determination of the annual boundaries is therefore usually uncertain. As an example, Hartig's[1] statement may be cited, that in the case of Willows and Poplars with a smooth cortex, the number of zones of bast-fibres is smaller than the age in years, amounting only to 3–4 for every 10–15 years, while, during the development of thick bark-forming cortices, 2–4 fibrous zones arise annually. The species of Acer[2] form in the first years either one, or (at the base of the annual layer) two, successive fibrous zones, but even from the sixth year onwards the relation changes in such a manner that often only 20–25 fibrous zones correspond to 100 years. The numbers are more regular in Tilia, where, according to Hartig[3], four fibrous zones appear at the base and one at the apex of the shoot in its first year, to which two or three are added in the second year, and in each succeeding year, on the average, two; this is also the case in Pyrus communis, which, according to Mohl[4], forms one fibrous zone annnally.

In those woody plants also, which renew their cortex every year, and in which the limit of the annual increment of growth is sharply defined by the layer of periderm formed at its outer side (Sect. 177), similar differences to those just mentioned appear. Lonicera Caprifolium and its allies annually form one zone of fibres and one of soft bast; Clematis Vitalba usually two of each[5]; Vitis vinifera generally forms two fibrous zones alternating with soft bast, at the close of the first period of vegetation, while in later years 3–5 are generally formed annually[6].

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[1] *l.c.* p. 444.
[2] *l.c.* p. 547.
[3] *l.c.* p. 560.
[4] Botan. Zeitg. 1855, p. 880.
[5] Hanstein, Baumrinde, pp. 72, 77.
[6] Hanstein, *l.c.* p. 61.—Von Mohl, *l.c.* p. 879.

CHAPTER XV.

SECONDARY CHANGES OUTSIDE THE ZONE OF THICKENING.

Sect. 168. In the normal Dicotyledons and Gymnosperms the mass of wood and bast developed from the cambium is bounded on the one hand by the pith, and the pre-existing ligneous zones adjacent to it, on the other by the external cortex and the pre-existing bast. It is clear, *a priori*, that this surrounding tissue may, and to some extent must, undergo changes, in consequence of the cambiogenetic secondary growth.

As stated above, no change in the *pith* is necessarily involved in the actual course of the processes of secondary growth described, or as a consequence of them. As a matter of fact, however, it has been asserted, especially by Duhamel[1], that in trees and shrubs the medullary cylinder diminishes in thickness, and may at last wholly disappear as the secondary growth of the wood proceeds. As regards the majority of cases, this view has been given up, as depending upon imperfect observation, and in fact the only demonstrable anatomical change in the pith during the phenomena of secondary growth is, that it sooner or later, rapidly or slowly, dies off and dries up. The possibility of a change in the pith caused directly by the growth in thickness is not indeed excluded *a priori*. For if wood and bast increase in thickness and circumference, and the external cortex does not yield to this enlargement of the circumference in a corresponding degree, an increasing pressure will be exercised on the pith, which may lead to anatomical changes in the latter. In what cases and in what form such changes may possibly take place, are questions which have not been investigated, and to the solution of which there is scarcely any safe clue; the possibilities will not be discussed here. That such cases occur is however shown by the change of form in the pith of the internodes of Aristolochia Sipho, which accompanies the growth in thickness. The young internode, up to the age of one year, has an approximately circular transverse section. The pith, which is of the same form, or is broadly elliptical, as seen in transverse section, consists, like the medullary rays, of permanently delicate and soft-walled cells, and is surrounded by a circle of 11–13 leaf-trace bundles[2], without intermediate strands. The external cortex enclosing the latter contains a strong

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[1] Physique des Arbres, I. p. 37; detailed discussion in De Candolle, Organographie, I. p. 168.

[2] Compare Nägeli, Beiträge, p. 82, Taf. VIII.

ring of sclerenchyma (p. 419), and is covered by the very tough epidermis, which is for a time persistent. The vascular bundles take an unequal share in the cambiogenetic growth in thickness, which makes a vigorous start in the next year. The median bundles of the two next higher leaves, occupying two diametrically opposite segments of the circle, and their next neighbours, grow less strongly in thickness than those situated in the two other segments; the increase is greatest in the three bundles which occupy the middle of each of the latter segments; it chiefly affects the xylem. During this unequal growth in thickness no perceptible change at first occurs in the form of the cross-section of the whole internode, and even at a later period the change is but trifling. On the other hand, those ligneous bundles, which grow more strongly than the others, press with their inner edges against the pith, the cells of which become compressed in the direction of the corresponding radii of the transverse section, and the general form of the pith is changed in such a manner that its transverse diameter, lying in the direction of the greatest growth in thickness, constantly becomes smaller, while the diameter at right angles to the latter remains unchanged. In an internode five or six years old the pith is merely a narrow band, the shorter diameter of which scarcely amounts to $\frac{1}{10}$ of the (original) longer one. The cause of these phenomena manifestly lies in the fact that the cortex undergoes too small an extension for the volume of the growing wood, and by its resistance presses the latter against the pith, and compresses it. Allied species of Aristolochia behave in a completely similar way.

The disorganisation of the pith in the shrubby species of Astragalus, which yield gum-tragacanth, may further be mentioned here, though not actually standing in direct causal connection with the anatomical processes accompanying growth in thickness[1]. It consists in the conversion of the cellulose-membranes into a mucilage which is capable of swelling up greatly; the change extends from the pith to the medullary rays, and chiefly affects the cells of the middle of the latter, and of the pith, while those which border on the ligneous strands are changed in a less degree, or not at all. In the living plant the mucilage is already present in a highly swollen condition, and is kept in high tension by the pressure of the surrounding resistent tissue[2]. On injury to these tissues it flows out, and when a plant is left to itself it may spontaneously burst the surrounding tissue, and exude from the cracks in the form of the strings which on drying form the tragacanth of commerce. In many species, e. g. A. rhodosemius, the mucilaginous disorganisation begins early, even immediately below the apex of the stem[3]; in others it appears to come on at a later period.

As regards the gradual dying off of the pith in old woody stems, the disappearance of the cell-contents, and especially of the store of starch, similar rules hold good to those for the formation of heart-wood. Comp. pp. 403 and 510.

Leaving out of consideration the displacements obviously occurring in the cases of Aristolochia and Astragalus, no anatomical changes in the *wood*, directly caused by the growth in thickness, are known. On the influence of the cortical pressure on the formation of autumn-wood, which is indirectly connected with the above, comp.

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[1] Von Mohl, Botan. Zeitg. 1857, p. 33. [2] Flückiger and Hanbury, Pharmacographia, p. 153.
[3] Graf zu Solms-Laubach, Botan. Zeitg. 1874, p. 69.

the remarks and citations upon p. 500; on the processes of degradation in wood when ageing, the relation of which to these phenomena is, to say the least, very doubtful, see Sect. 154. The primary medullary bundles of the forms here in question—Piperaceæ, Begoniæ, Araliæ and Umbelliferæ, Mamillariæ, and Melastomaceæ (comp. Sect. 62)—undergo, so far as is known, no secondary anatomical changes.

Sect. 169. All the parts lying outside the active cambial zone, namely, the *entire primary cortex* and *the secondary cortex for the time being*, necessarily undergo progressive changes with the progressive growth in thickness. These consist in—

(*a*) Growth of existing tissue-elements, new formation of equivalent ones from them, and subsequent metamorphosis (p. 5): Sects. 170, 171.

(*b*) Compression, displacement, and destruction of existing tissues: Sects. 172, 173.

(*c*) New formation of non-equivalent forms of tissue out of existing ones: Periderm, Sects. 174–179.

The process indicated by (*a*) only affects the cellular tissues: Epidermis and Parenchyma.

Sect. 170. In the majority of the cases of vigorous growth in thickness, the *epidermis* is destroyed at an early period, cork or bark being formed; further details will be given below. Stems, however, are not wanting, whether with weak or with very vigorous growth in thickness, in which the epidermis follows the latter by its own growth during a considerable period. This is the case in many herbaceous plants, and in woody plants with a smooth, green, cortical surface, as long as the latter is present. The condition of the surface mentioned is in fact dependent on the persistency of the epidermis, the cells of which, being filled with sap, allow the colour of the sub-epidermal chlorophyll to show through. As examples of stems and branches with vigorous secondary growth of the wood, which, for some years at least, retain the epidermis, may be mentioned: Viscum album[1], species of Ilex, the evergreen Jasmines, Menispermum canadense, Aristolochia Sipho and allies, Sophora japonica, Negundo, and many others. In Acer striatum the epidermis is still for the most part present in a living condition, and following the growth, even on stems a foot thick, and forty years or more old.

The long-lived epidermis of the woody plants mentioned is provided from the first with thick strongly cuticularised outer walls, which sometimes contain and excrete a large amount of wax (comp. pp. 76, 82). Its original structure undergoes relatively unimportant changes during growth. These consist in an increased thickening of the cuticularised external walls, the surface of which covered by the cuticle usually remains smooth; but in Acer striatum as well as in Negundo and Sophora japonica it becomes cracked as the thickening proceeds, the cracks penetrating from outside into the external cuticular layers, which do not follow the growth, and successively breaking them up into crumbling fragments. In Acer striatum the cracks coincide with the dilated bands of the external cortex, to be described below; and a new excretion of wax rods takes place in each case on the surfaces newly laid bare by the cracks; it is on this that the white striation of the cortical surface

[1] Von Mohl, Botan. Zeitg. 1859, p. 593.

depends[1]. In addition to these changes, the growing epidermal cells, as they become larger in the direction of the circumference, i. e. broader, divide successively by walls which stand at right angles to their transverse diameter, and to the surface, and abut on the inner surface of the original wall. This successive multiplication of the epidermal cells takes place in such a degree, that the average breadth and general form of the individual cells remain approximately the same, or only undergo inconsiderable changes. The epidermal cells of the stem of Acer striatum when the latter is 200^{mm} thick, are, for example, scarcely twice as broad as those of a shoot one year old, and 5^{mm} in diameter.

Sect. 171. **Parenchyma** forms the main mass of the primary external cortex, the medullary rays of various degrees in the bast-layer, and the parenchymatous groups in the bundles of the latter. Until a zone of cortex is thrown off by the formation of bark, which may take place sooner or later, but in many instances never occurs at all, and which will be discussed below, the parenchyma follows the cambiogenetic secondary growth by corresponding growth of its own, in all the parts in which it exists. The parenchymatous mantle of the external cortex increases successively in width, while the medullary rays of the bast, and the parenchymatous elements of the bundles, increase in breadth in the centrifugal direction (Fig. 214, p. 528). The several portions of the bast do not always participate in the same degree in this phenomenon, which may shortly be termed *Dilatation* of the parenchyma. If attention be directed to cases of extreme difference, it is found that in the one case dilatation of the entire parenchyma of the bast takes place in an approximately uniform proportion, as each annular zone becomes shifted outwards. In all the radial bands, and thus most clearly in the medullary rays of every degree, the parenchymatous cells increase uniformly, and quite gradually in breadth, in the centrifugal direction. The intermediate non-equivalent tissues, which do not grow with them, especially sieve-tubes and bast-fibres, thus become uniformly removed one from another, and the more so the further they are from the cambium; as in Salix fragilis and allies, Punica, Rhamnus Frangula[2], Spiræa ulmifolia, Pyrus communis, and Æsculus. In the other extreme case the dilatation is unequal in the various radial bands of the transverse section; it amounts to little or nothing in the bundles, and is most active, either in all the parenchymatous rays, or in some of them. Between the lateral limits of these dilated rays the arrangement, and lateral distance from one another of all elements of the tissues, remains approximately the same. This behaviour occurs, firstly, in a number of stems, which are constructed on the type described at p. 455, and the large medullary rays of which are broad and multiseriate; e. g. stems of Menispermum, Aristolochia, and Piperaceæ; here the dilatation is brought about, at least to the greatest extent, by the large medullary rays, and, indeed, the latter all take an approximately uniform share in the process, in their entire height. The strands of bast therefore remain similar in form and arrangement to the phloem portions of the original vascular bundles, from the further development of which they have arisen. They are not, however, wholly without share in the dilatation, as a slight

[1] For details compare Botan. Zeitg. 1871, p. 605, &c.

[2] Compare Berg, Atlas, Taf. 39, 40.

widening of their parenchymatous elements, and through them of the whole bundle, takes place here also. This category includes Tilia, and other woody plants provided with a similarly grouped bast. In young shoots of Tilia the zone of wood and bast is traversed by numerous large parenchymatous rays extending to the pith, most of which are uniseriate, but many, e. g. in transverse sections of a branch of Tilia parviflora now before me, the seventh, ninth, or fourth, and so on, are bi- or triseriate; the latter is at any rate the case at the cambial limit, and sometimes as far as the pith, while in other cases they become uniseriate before reaching the latter. The dilatation begins in the biseriate and triseriate rays; whatever strands and rays lie between them, take, in the first instance, no part in the process. As growth in thickness proceeds, a constantly increasing number of the original uniseriate rays take part in the dilatation. Later on successive small secondary rays are also involved in it. When a ray takes part in the dilatation it is, as a rule, bi- or pluriseriate at the cambial boundary. The result of these phenomena is in the first instance the severance of the bast-layer into the often described[1] groups of bundles with a wedge-like form widened towards the cambium, as seen in cross-section, and rays, alternating with the former, widened in the opposite direction, and further, the successively occurring subdivision of the first groups of bundles into more numerous narrower ones, separated by rays. The number of groups in a transverse section, rises, for example, in branches of T. argentea now before me, from 45, in an internode 6^{mm} thick, to 138 in one 28^{mm} thick. In order to complete this description, which has been given in the first instance with reference to the transverse section, it must be added that the medullary rays are of considerable height—the larger ones measuring more than a hundred cells—and their ends situated in quite different transverse sections all round the stem; and that the dilatation begins in every ray about at the middle of its height, and thence advances upwards and downwards.

Quite similar phenomena to those in the bast of the Lime reappear in many other plants, and in members of different value, e. g. in the stem and branches of Hibiscus syriacus, Pterocarya, and Galipea officinalis, and in the highly parenchymatous roots of Umbelliferæ (Archangelica, Levisticum, &c.), Glycyrrhiza, and many others[2].

Intermediate cases between the extremes, represented on the one hand by Salix fragilis, Spiræa ulmifolia, and Punica, and on the other by Tilia and Menispermum, would naturally be expected to occur from what has been stated. In these every transverse section shows radial bands of the bast, which are more or less strongly dilated, in various gradations. Examples are afforded by Sparmannia africana, represented in Fig. 214, p. 528, with numerous strongly dilated rays, and more slightly dilated ones in the divisions limited by them; further, in very various gradations, by the Quinine barks, Croton Eluteria, Simaruba officinalis, Cinnamomum zeylanicum, &c.[3]

In the structure of the dilated masses of parenchyma the increase in the

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[1] Compare e. g. Schacht, Der Baum, p. 198; Lehrb. II. p. 50.—Hanstein, Baumrinde, Taf. I.
[2] Compare Berg, Atlas, Taf. 37. 6, 8, 9.
[3] Berg, *l. c.* Tab. 29–38.

tangential diameter, or breadth, of all cells taking part in the dilatation, is most conspicuous, and follows obviously from what has been stated. In proportion, however, to the increase in breadth, successive radial bipartitions take place, by means of which the original breadth of the cells is approximately restored, and the number of the cells in each tangential row increased in a corresponding degree. These phenomena also take place in the endodermis of the stems, mentioned at pp. 121 and 415, and of the roots, so long as it is not thrown off and thus excluded from the growth. An increase in the average breadth of the individual cell no doubt takes place, judging from estimates. It appears to rise rapidly to an approximately constant value, and then to maintain this during the succeeding divisions, so that cells of the same layer in a stem a foot thick are no broader than in one as thick as one's finger, though they are of course more numerous in a corresponding degree. The final, constant, average dimensions are relatively little in excess of those existing originally at the beginning of growth in thickness; they may be estimated to amount to scarcely more than two or three times the latter. Accurate measurements are still to be undertaken. Cell-division in directions other than the radial, resulting in a multiplication of the concentric layers of parenchyma, is rare, at least in the cortex of those woody plants which have been principally investigated, and apart from the formation of periderms: those special cases in which it does occur will be discussed below (Sect. 172); it remains to be investigated whether or not such division also takes place in many fleshy roots.

The structure of the cell-walls and of the contents, the periodic variation in the amount of starch in the latter, &c., remain the same in the principal mass of the parenchyma during the dilatational changes, in certain cases throughout life, in others for a time. Sooner or later, however, changes may occur, and in fact (*a*) dilatational changes of the collenchymatous hypodermal layers (p. 404), and (*b*) processes of secondary sclerosis.

The *collenchymatous hypodermal layers* of the cortex of stem and branches in woody plants always follow the dilatation uniformly for a time in their whole circumference, while they maintain their original characteristic structure; this process often continues uniformly, so long as they are not thrown off by the formation of bark; the question whether, in many cases, their walls decrease somewhat in thickness, as the extension proceeds, remains to be more accurately investigated. In some cases, which might no doubt be multiplied by further observations, namely, in Tilia, Acer striatum, and Æsculus, other conditions prevail. At certain points the collenchymatous cells show a considerably greater growth in breadth than in the intermediate tracts, and all their walls, both those originally existing and the portions added by subsequent growth, decrease considerably in thickness. They permanently assume the appearance of thin cellulose-walls, and are thus sharply distinguished from the neighbouring thick, brilliant, collenchymatous walls. With this is connected, at least in the case of Acer striatum, a diminution in the amount of chlorophyll, which is apparent to the naked eye. The process begins in a few small portions of each transverse section, spreads laterally from these points, and involves new regions lying between the first. The thick-walled collenchyma in this way becomes subdivided into constantly smaller portions, lying isolated among the altered tissue, and at last disappears, as these portions also become involved in the process

of transformation. Until this occurs the external cortex appears traversed by the altered bands, which I have already termed elsewhere 'dilatational bands[1].' Their occurrence indicates an unequal participation of alternate bands of the cortex in the dilatation, and this will find its explanation in dissimilar mechanical conditions, which are still to be more minutely studied. In Tilia the first dilatational bands of the external cortex correspond exactly to the most dilated medullary rays; in Acer striatum they often coincide with the intermediate spaces between the outermost bundles of bast-fibres, which are filled with parenchyma, but they do not occupy this position exactly or constantly.

In the peripheral layers corresponding to the original collenchyma the connection of the cells remains close and approximately unbroken, if the local interruptions due to the lenticels, to be described below, be left out of consideration. In the inner, lacunar, portion of the external cortex the cavities originally existing grow in the direction of the dilatation. Further, and often extensive, interruptions of continuity may be produced both in the region indicated, and also, though less frequently, in the more deeply situated layers of the bast, as the effect of the tension, distortion, and pressure which the tissues undergo during growth in thickness. In proportion to the originally lacunar structure of the external cortex, it therefore becomes traversed to an increasing extent, as dilatation proceeds, by broad, crevice-shaped cavities, and is often split up into irregular concentric lamellæ, e. g. species of Prunus and Pyrus, Æsculus, &c. A similar subdivision into lamellæ is shown, for example, by the bast-zone in Berberis and Mahonia. In addition to this, radial cracks appear in the bast in several cases, especially in the species of Prunus; they are situated along the lateral boundaries of the medullary rays, and increase in width towards the outside, because the cells of the rays, while usually remaining in connection among themselves, grow in breadth to a much smaller extent than the rest of the cortex, and a severance therefore ensues in the lateral limiting surfaces between rays and bundles.

Secondary Sclerosis is the name given to the phenomenon that individual cells, or definite groups of cells of the parenchyma, assume the sclerenchymatous character after the differentiation of tissues is complete, often thickening their walls to an immense extent during lignification, at the expense of the internal cavity. During this process they sometimes approximately maintain their original form (short sclerenchyma, stone-sclerenchyma), while they sometimes undergo considerable changes of shape and size (many-armed stone-sclerenchyma).

These phenomena occur principally in very persistent portions of the cortex of woody plants, in some to a very large extent, in others to a less extent or not at all. The actual structure and the strength of the older cortices are in a high degree influenced by this process. Conspicuous as these structures are, and often as they have been described, yet the history of their origin is still much in want of more accurate investigation.

The limiting zone between the external cortex and the bast-layer is, in the first instance, the special region of these stony formations, and is also usually first in point of time. In numerous woody plants, which in this zone form sclerenchymatous

[1] Botan. Zeitg. 1871, p. 605.

fibres—the bast-fibres corresponding to the primary vascular bundles—a one- or many-layered zone of parenchyma, connecting the former into a closed ring, becomes converted into stone-sclerenchyma. A ring thus arises, composed partly of fibrous bundles or scattered fibres, and partly of short sclerenchyma, which traverses the border-zone indicated, and is either completely closed at an early period (e. g. Cinnamomum zeylanicum and Fagus), or remains locally interrupted by thin-walled parenchyma for a considerable time, even for years (e. g. Betula alba). Examples of this occurrence of the compound sclerenchymatous ring are afforded, besides the plants mentioned, by Quercus pedunculata, Q. Suber, Carpinus, Corylus, Fraxinus excelsior, Juglans regia, Gymnocladus canadensis, Koelreuteria, Negundo, Laurus nobilis, species of Cinnamomum, and many others. In Fraxinus excelsior a compound sclerenchymatous ring, similar in its composition to the first, may arise at a later period in the secondary bast.

In Fagus silvatica, Quercus Suber, &c., the first sclerenchymatous ring soon acquires projections directed towards the larger medullary rays. In the one-year-old shoot of the tree first mentioned, it shows, opposite each large medullary ray, a protrusion of the adjoining portion of the ring, which here consists of stone-elements uniting the fibrous bundles. The protrusion projects inwards like a ridge up to the neighbourhood of the boundary of the cambium. As growth in thickness goes on, these projecting ridges of sclerenchyma are not only persistent, but increase in the radial direction in such a manner, that opposite each medullary ray they penetrate into the wood beyond the cambial boundary, running between the strands of wood and bast. The cambial boundary is therefore deeply and sharply indented at the medullary rays indicated. The elements of the cortical rays produced by the cambium in this indentation immediately become sclerenchymatous, so that a sclerenchymatous ridge is fitted into the depression. In the medullary rays successively developed at a later period the same process takes place, with the sole difference that their sclerenchymatous ridges do not extend so far as the external ring. If the cortex of the older stems be torn off from the wood at the boundary of the cambium, the hard ridges of the medullary rays stand out on its inner surface like little combs.

Similar sclerenchymatous ridges, projecting into the medullary rays, occur without original connection with the compound sclerenchymatous ring, in Platanus and Casuarina. They represent the second case of the formation of stone-sclerenchyma in a definite region.

In the third case, finally, cells take part in the sclerosis, which may be scattered in all parts of the external cortex and secondary bast. They sometimes occur isolated in tissue which remains soft, e. g. in the outer portion of the bast of Punica Granatum, when six years old; gigantic scattered sclerenchymatous elements (p. 145) in the bast of the root of the same tree; 'stone-cells' in the external cortex of the Cinchonæ, Simaruba, &c. In other cases they form larger groups, nests, annular segments, &c., inserted in the soft tissue, the number and size of which may increase in the older parts of the cortex to such an extent that they form its principal mass, so that the old cortex has been appropriately termed 'stone-bark' by Hartig. Casuarina, Platanus, species of Quercus, Betula, Fraxinus, and Acer, the White Fir, also Æsculus Hippocastanum, and especially Fagus silvatica, may be mentioned as typical examples of this structure.

The phenomena of sclerosis now described appear in woody plants, to some extent in immediate continuity with the primary differentiation of tissues, and coincide with the first beginning of secondary growth in thickness; these cases, especially the formation of sclerenchymatous rings at the limit of the external cortex, could not, if they stood alone, be considered under the head of secondary formations. Other phenomena, however, are so intimately connected with the former, that they could scarcely be separated in the description, and these affect tissue-elements which have often belonged for years to a definite differentiated tissue, namely, the parenchyma, and only subsequently become involved in the sclerosis. The first sclerenchymatous ring of the Beech, though it originates in the first period of vegetation, increases every year in mass as it becomes shifted outwards during the growth in thickness, owing to the fact that both those parenchymatous cells which border on it externally, and others which are interpolated between its elements, in a manner to be explained below, successively undergo sclerosis. The ridges of the medullary rays arising from it constantly become broader, owing to the same process, the further they are shifted outwards. According to Mohl and Sanio[1], the compound sclerenchymatous ring of Quercus Suber behaves in the same way. In the secondary bast of the Beech, the White Fir, and other trees, sclerotic elements are absent for at least 1–2 years. As each zone becomes shifted outwards, these elements then appear in it in increasing numbers. The external cortex of the Beech, the Horse-chestnut, and the White Fir is, in the first year, and often no doubt during several years, free from sclerenchymatous elements, while in later years it is abundantly permeated by them. Similar conditions prevail in the external cortex and bast-layer of Drimys Winteri, and many other plants.

So far as the existing data admit of a decision, the elements which are affected by the secondary sclerosis always belong to the parenchyma, as was stated above; they may have discharged the functions of parenchymatous cells for years. Their form and size appears in many cases not to be essentially changed on the occurrence of sclerosis (e. g. cortex of Fagus); in others a considerable alteration of growth and form appears simultaneously with the commencement of this process. This is most conspicuously the case with the many-armed, ramified, sclerenchymatous elements of Abies pectinata, the arms of which are closely pectinated, forming as it were a felt; so far as is known, they originally proceed from polyhedral or prismatic parenchymatous cells, both of the external cortex and of the secondary bast.

Sect. 172. Sieve-tubes, milk-tubes, sclerenchymatous elements, and sacs containing crystals or other secretions, are, from their differentiation onwards, incapable of further growth. They behave passively on dilatation, and become displaced from their original position by the latter process. The longitudinal secretory canals also share in the displacement, the tissue immediately surrounding them usually becoming widened through the dilatation. In so far as the process of dilatation acts alone, the displacement consists in a progressive lateral separation of the elements mentioned, or of the strands into which they are united, and of the canals. If, as is often the case, resistance is offered to the dilatation through the elasticity of the superficial

[1] Von Mohl, Verm. Schr. p. 220.—Sanio, Pringsheim's Jahrb. II. p. 73.

cortical layers for the time being, e. g. epidermis, external cortex and periderm, the simple dilatational displacements are accompanied by others, the special forms of which, varying greatly according to the special cases, need not be more minutely described.

The resistent, sclerenchymatous elements, and also the crystal-sacs, do not undergo any essential alteration of their structure during this process. Those provided with soft walls, especially the sieve-tubes, and also many long secretory sacs, suffer changes, simultaneously with the displacement, which, in general, consist in the disappearance of the contents and collapse of the walls, and may be shortly termed Obliteration. As this takes place under the joint action of the pressure exercised in the radial and tangential directions, proceeding from the dilatation and the resistance of the surface, it is obviously suggested to find in this the cause of the obliteration. It is questionable, however, whether a change in the obliterating organs, and especially in their contents, independent of the pressure, is not the primary cause of the phenomenon, and the pressure only a co-operating cause.

The obliterated sieve-tubes appear laterally compressed, even to the disappearance of their lumen. Their structure, including that of the ends of their members which bear the sieves, becomes indistinct, and may even be wholly unrecognisable; their walls appear slightly swollen, but no measurements have been made which actually prove any swelling. Where the tubes are isolated, they are easily overlooked after their collapse, seeming, at the first glance, to have quite disappeared. Where they are united to form larger groups, their membranes appear collectively in sections, especially transverse sections, as a homogeneous, gelatinous mass (like dry gristle or horn), in which the compressed cavities are visible as narrow crooked cracks or marks, the original lateral limits as indistinct lines. Similar appearances have already been described on p. 325, and represented in Fig. 158, p. 336, in the case of the primitive sieve-tubes of the vascular bundles. As the phenomenon described often extends with apparent uniformity over the entire transverse section of a considerable group of sieve-tubes, the question, how far the cambiform cells which originally accompany the tubes, also share in the obliteration, remains to be investigated.

Obliterated groups of sieve-tubes have been described by Wigand[1] as 'horn-bast,' while their origin and significance have been clearly represented by Rauwenhoff[2].

The obliteration of the sieve-tubes begins in the oldest external zones of the cortex, and advances, with the dilatation, in the centripetal direction. It seems to come on more or less gradually or suddenly according to the particular case, a point on which more minute investigations still remain to be undertaken.

The obliteration of the secretory sacs has been described by Vogl[3] in the case of the large sacs of the Cinchona-bark. These apparently lose their original contents

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[1] Pringsheim's Jahrb. III. p. 118.

[2] Nederlandsch Kriudk.-Archief, V. p. 23. Compare also the treatise by the same author, Sur les caractères et la formation du liége, &c., reprinted in the Ann. Sci. Nat. 4 sér. tom. XV., and in other places.

[3] Die Chinarinden d. Wiener Grosshandels, p. 12.

and collapse, and the cavity thus formed is filled up by luxuriant growth of the surrounding, dividing parenchymatous cells, until the wall of the sac may even disappear.

It has already been stated that those elements which are passive during dilatation, remain in their original close connection one with another during the process of separation, if they are united into strands. If, on the other hand, as is in fact often the case with the sclerenchyma, they form closed annular layers, the latter are burst. The severance of connection then takes place through the limiting surfaces of the elements. As soon as this begins at any point of the external surface of a sclerenchymatous ring, neighbouring parenchymatous cells bulge out and insert themselves into the gap, which they fill up. They then either maintain the properties of parenchymatous cells, growing and dividing in proportion to the increasing width of the gap owing to progressive growth in thickness, or they undergo the sclerenchymatous metamorphosis immediately upon their insertion; the original ring becomes completed by interpolated short stone-elements, as described above.

The latter process occurs in the stony or compound sclerenchymatous rings, which, e. g. in the Beech, always remain closed without any growth of the existing sclerotic elements, while their circumference constantly increases. The former case may occur in the same rings, and takes place especially in rings of fibrous sclerenchyma, where the latter are not thrown off at an early period by internal formation of periderm, as is usually the case; e. g. the bulky fibrous ring of Aristolochia Sipho, thick foliage-stems of Gypsophila altissima, and, in a lesser degree, in old thick stems of the Gourd. In the above-mentioned Aristolochia especially, the ring is first burst at the places lying opposite the bands of greatest dilatation, and then at a constantly increasing number of other points, and is thus broken up into segments, which are always becoming smaller, and finally often consist only of single separated fibres, the space between them being filled up by thin-walled parenchyma, which follows the dilatation. In this case also, however, a partial completion of the ring by short stone-sclerenchyma may take place, owing to secondary sclerosis.

Sect. 173. The generally distributed phenomena of displacement and obliteration may be accompanied in special cases by processes of disorganisation, and the latter may extend to tissues of every kind. In the cortex of the Amygdaleæ, e. g. Prunus avium, groups of tissue of varying extent become disorganised, and converted into cavities filled with gum and bassorin, from which the swelling contents, consisting of cherry-gum, finally exude through the bursting surface of the cortex. According to Wigand's statement[1], it is chiefly the obliterated sieve-tubes in the cortex from which this disorganisation starts, and then further extends throughout the non-equivalent tissues. On the other hand, the latter also, especially groups of thick-walled parenchymatous cells which have been called abnormal, are certainly starting-points of the gummy disorganisation. On the very various special phenomena, which may, for the most part, belong to the province of Pathology, comp. Wigand's description.

In the older cortex of many Coniferæ, besides the protogenetic reservoirs of resin (p. 441), and to some extent as a substitute for the latter when they have been lost owing to formation of bark, reservoirs filled with balsam appear, which were termed

[1] *l. c.* p. 130.

by Mohl[1] resin-cavities; their origin is no doubt always lysigenetic, resulting from a disorganisation of definite groups of tissue. Among the Abietineæ investigated by Mohl their formation is wholly absent in several species, namely, Pinus sylvestris and nigricans, Abies excelsa and pectinata; they appear in Larix europæa, Abies sibirica, and Pinus Strobus; in the first-mentioned tree in the first year, in the two others not before the eighth or tenth year of life, in the cases investigated. The seat of their occurrence is especially, and in Larix and Abies sibirica exclusively, the external cortex, in P. Strobus the bast also. As years go on they increase in number, and the pre-existing ones in size; the transverse diameter is, for example, stated by Mohl, in the case of Larix europæa, at little more than $\frac{1}{10}$mm in a young cavity one year old, and at almost 1mm in a cavity eighteen years old. According to Mohl, the form of these cavities in the trees mentioned is at first approximately spherical, and afterwards passes over into a lenticular, transversely elongated form. Their origin and enlargement by the solution of definite groups of tissue has not indeed been described in detail, but scarcely admits of doubt, especially after Wigand's statement[2], according to which they arise in the bast of Pinus Strobus from the solution of groups of tissue, which contain obliterated sieve-tubes, parenchyma, and stone-sclerenchyma.

The mode of origin stated by Wigand to occur in Pinus Strobus, doubtless applies to the cavities filled with resin, which appear in the form of longitudinal canals, ending, so far as can be asserted, blindly, in the older bast of the Cupressineæ (Juniperus communis, Thuja, Biota, and Cupressus spec., comp. p. 443). Their formation begins here[3], at points in the older zones of bast which cannot be more exactly indicated, while the latter are still turgescent, and still contain non-obliterated sieve-tubes; resin first makes its appearance in isolated, otherwise unaltered, parenchymatous cells, both in the bundles and in the medullary rays; the resiniferous cavity then arises by means of an increase in the amount of resin, and successive solution of the membranes, which perhaps themselves afford material for the formation of resin; this cavity becomes widened by the extension of the same process within a constantly increasing circuit, and over all the surrounding tissue-elements of the bast, sieve-tubes and fibres not excepted. In the parenchymatous cells bordering the passage, a considerable enlargement in the radial direction occurs in the case of Juniperus, with papillose protrusions towards the passage, while isolated divisions by tangential walls are also frequent.

Periderm[4].

Sect. 174. In addition to the changes in the growing cortical mantle already described, more profound ones ensue on the new formation of the phellogenetic, i. e. cork-producing meristem, and its products. It may be expedient to include all

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[1] Botan. Zeitg. 1859, p. 333. [2] *l. c.* p. 166. [3] Frank, Beitr. p. 122.

[4] Von Mohl, Unters. üb. d. Entwickelung des Korkes und der Borke auf der Rinde der baumartigen Dicotylen; Diss. 1836.—Verm. Schriften, p. 212.—Hanstein, Unters. üb. d. Bau u. d. Entw. d. Baumrinde; Berlin, 1853.—Sanio, Unters. üb. d. Bau u. d. Entw. d. Korkes, Pringsheim's Jahrb. II. p. 39.

the latter and their meristem with them under one general name, and to choose Mohl's old term *Periderm*, with a modification of its original meaning, comp. p. 114.

The peridermal structures always arise in a layer of cells which has already been differentiated. This is their initial layer, and is either formed by the single-layered epidermis, or by a single sub-epidermal layer of parenchymatous cells, which may occur at various depths, and runs approximately parallel to the surface of the part. The periderm consists of the *phellogenetic meristem*, and the tissues that have been derived from it, which, in all cases, include a single or many-layered stratum of *Cork-cells* or *Cork-tissue*, to which usually, but not always, *phellogenic* or *peridermal parenchyma*, the *Phelloderm* of Sanio, is added.

If a layer of cork is formed in the interior of a mass of tissue, the tissue lying outside it dries up, and is eventually thrown off as *bark* (Rhytidoma, Mohl). The formation of bark is the immediate consequence of the internal formation of periderm, and the name is as a rule employed for the dried-up tissues and the adjacent peridermal layers conjointly; with the formation of periderm that of the lenticels stands in the closest connection, but the consideration of the latter, on account of certain peculiarities, will be omitted here, and deferred to Sect. 179.

The general course of the formation of periderm has to a great extent already been stated in Sect. 24. The initial layer of cells becomes converted by tangential divisions into a multiseriate zone, the elements of which partly remain meristematic, and partly pass over into tissue. So far, and so long as the former is the case, they have the capacity of following the dilatational growth by means of their increase in size, and successive radial divisions occur in them, as in the cells of the dilated parenchyma, by means of which the original average breadth is always again approximately restored. Accordingly, all cells belonging to the periderm are arranged in radial rows, each of which originally corresponds to one of the initial cells, and may become successively doubled, and they further form concentric (tangential) layers, see Fig. 216.

In the course of the tangential divisions in an initial cell and the radial row derived from it, two extreme forms may in the first instance be distinguished, which, after Sanio, are termed the *centripetal* and *centrifugal* forms; besides these, there is the mode of succession which proceeds alternately in the centrifugal and centripetal directions, and may be generally termed *reciprocal*.

In the centripetal succession the initial cell is divided into two daughter-cells, the outer becomes a tissue-cell, the inner remains meristematic, and continues the same process in such a manner that, in the further successive bipartitions, the inner cell always remains meristematic, while the outer becomes tissue.

In the second case the order is reversed. Of the products of the successive tangential divisions the outer cell always remains meristematic, while the inner becomes an element of the tissue.

In the reciprocal succession (Figs. 216–218) the division begins in one of the orders mentioned, then changes over into the other, and may then again change back to the first. At the first origin of the phellogenetic layers Sanio found the following cases of reciprocal succession:—

1. The first two divisions in centripetal order, then the innermost cell becomes a tissue-cell, the second from the inside becoming a meristematic cell; after the third

division they go on in the centripetal order, comp. Figs. 216, 217 ('centripetal-intermediate order').

2. Division begins centrifugally, and then changes over to the centripetal order. If the latter takes place immediately on the third division, in such a manner that the second cell from the inside then becomes the meristematic cell, which henceforth divides centripetally, Sanio calls the process centrifugal-intermediate; if the reversal only takes place after later divisions, Sanio calls the order centrifugal-reciprocal.

In the later stages of growth of those phellogenetic meristems which are active for a long time, the reversal of the mainly centripetal order into the centrifugal, and its immediate return to the centripetal, take place in most cases from time to time without strict regularity.

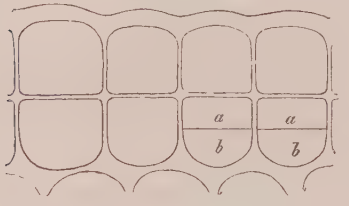

Fig. 216

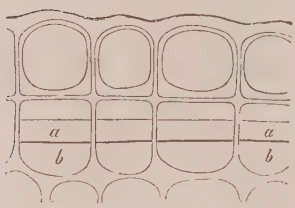

Fig. 217.

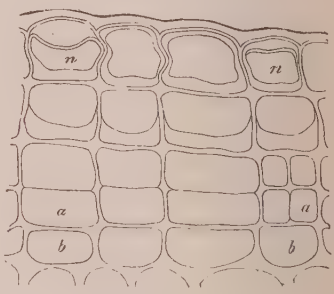

Fig. 218.

FIGS. 216—218.—Transverse section through the surface of a branch of Sorbus Aucuparia. After Sanio. Origin of the periderm.—Fig. 216. Four epidermal cells, already divided once tangentially; in the two pairs to the right the lower cell is once more divided into *a* and *b*. *a* meristematic cell, *b* phelloderm.—Fig. 217. Further stage of development; *a*—*a* meristem, *b*—*b* phelloderm. The cork-cells corresponding to the outer halves of the epidermal cells have acquired strongly thickened walls.—Fig. 218. Still further developed stage; *a*—*a*, *b*—*b*, as in the former figure. Outside *a*—*a* are three layers of cork-cells, the two outer ones with thickened walls; at *n*, *n* the inner layer of the wall is partially released from the limiting lamella. To the right, at *a*, the radial division of a peridermal row is beginning.

Whatever the course of the divisions may be, it is nearly always only one cell of each radial row, and consequently only one layer of cells in the entire peridermal zone, which remains in the meristematic condition, so as to carry on the divisions; all other cells directly become elements of the tissue, after they have originated by division in the meristem. An exception to this rule has only been observed with certainty in the case of Philadelphus coronarius[1], and in this case the division in general proceeds centripetally, the innermost layer of cells remaining meristematic, but in each of those products of division which are given off externally, one or two tangential divisions (in the latter case proceeding centrifugally) take place, and only after this does the development of their products into tissue occur. According to Sanio, a similar process

[1] Compare Sanio, *l.c.* p. 99.

appears also to take place on the formation of the first layer of cork in Melaleuca styphelioides.

As will be shown in greater detail below, the duration and productiveness of a cork-meristem, when once formed, are remarkably various in the special cases. It may remain active for decades of years, and longer, and produce masses of tissue; and, on the other hand, its generative activity may come to a standstill after a few divisions, and it may itself, together with the layers it has produced, become converted into a permanent form of tissue.

It may happen exceptionally, and in no known case as a phenomenon of normal development, that in layers of meristem with persistent growth the cell which typically remains meristematic becomes a cork-cell incapable of division. The meristematic properties and functions are then transferred to the next inner parenchymatous cell.

The origin of the two forms of tissue derived from the phellogenetic meristem, when the latter remains permanently active, is determined in such a manner, that all cells formed on its outer side become *cork-cells*, while those formed on its inner side become *phelloderm*. Thus purely centripetal phellogens only form cork-cells, while reciprocal ones form the latter on the one side, and phelloderm on the other. Permanently active, purely centrifugal meristems, if they existed, would accordingly only form phelloderm. The occurrence of the purely centrifugal course of division is, however, limited to cases in which activity soon ceases, and in these cases either the inner of the few layers produced become phelloderm, and the outer cork-cells (Lonicera Caprifolium), or they are all converted into cork-cells.

The cells of the *meristematic layer* generally show the structure indicated by this term; individual peculiarities, e.g. the presence of chlorophyll in Sambucus nigra, and lateral thickening of the walls in Salix, &c., scarcely need to be mentioned here. Their form is that of polygonal plates, the transverse and longitudinal sections being more or less sharply quadrangular, and the radial diameter, as a rule, considerably shorter than the others.

The properties of the *phellogenic cortical parenchyma*, or *phelloderm*, are in all essential points similar to those of the outer dense parenchyma of the cortex; like the latter, it shows the phenomena of dilatation and sclerosis. The one generally applicable distinction from the latter consists in its origin as a supplementary structure added subsequently by the phellogenetic meristem, and in its radial arrangement resulting from its mode of origin.

The structure of the *cork-cells* has been dealt with in Sect. 24, p. 108.

The changes which are produced by the phellogenetic formations in the whole primary and secondary cortex depend upon their place of origin and special character. Three principal phenomena are accordingly to be distinguished, namely the *formation of superficial periderm*, of *internal periderm* and *bark*, and of Lenticels. It follows from the nature of the subject that these three kinds of structure are nearly related to one another, and therefore that transitions may also appear between them.

Sect. 175. *Superficial periderm.* In most stems of woody plants, in tubers, and also in some few roots, as those of Anisostichus (Bignonia) capreolata, and the Clusiaceæ[1], the epidermis is replaced by a periderm arising within or close beneath

[1] Van Tieghem, Ann. Sci. Nat., 5 sér. tom. XIII. p. 258.

it, the meristem of which remains active for a long time, and, as its principal product, forms a coating of cork. In most cases this formation of periderm begins simultaneously with, soon after, or even before the complete extension of the internode; in the plants mentioned above, p. 535, with a long-lived epidermis, it begins later, and often not for many years.

In a large minority of the cases the initial layer of the periderm is the epidermis itself: Nerium Oleander, Viburnum Lantana, lantanoides, prunifolium, all Pomaceæ (Figs. 216–218), Virgilia lutea, Staphylea pinnata, Solanum Dulcamara, all investigated species of Salix (Sanio), Euphorbia antiquorum[1], Melastoma cymosum, and Centradenia floribundum[2]. The formation of periderm in Acer striatum, which does not usually occur for many years, may also be mentioned here. In these cases only the original external wall of the epidermal cells is cut off by the phellogenetic layer; it is burst, and left to peel away gradually.

In the very great majority of the plants belonging to this category the layer of cells lying immediately below the epidermis is the initial layer for the formation of periderm (comp. Fig. 214, p. 528, and below, Fig. 223). The whole epidermis above it is burst and thrown off. Examples: Platanus, Acer campestre, Abies pectinata, Hakea florida;—Fagus silvatica, Rhamnus Frangula, Quercus Suber, Q. pedunculata, Castanea, Ostrya, Carpinus, Corylus, Betula, Alnus, Ulmus, Juglans, Celtis, Sambucus nigra, Plectranthus amboinensis, Crassula tetragona, Acer pseudoplatanus, A. platanoides, Tilia, Catalpa, Fraxinus, Syringa, Prunus, Amygdalus, species of Rhamnus, Viburnum Opulus, V. Oxycoccos, Populus; Medinilla farinosa, Miconia chrysoneura[3], and many others.

Closely connected with these cases is the appearance of phellogenetic divisions in the second or third sub-epidermal layer, observed in Robinia pseudacacia, Gleditschia triacanthos, and Cytisus Laburnum. In this case one or two external layers are thrown off, together with the epidermis, as a small bark.

In the simplest but rarer cases only cork-cells are produced in these peridermal formations, and the phellogenetic layer of meristem is reproduced by divisions in purely centripetal order, phelloderm not being formed. This is the case in Nerium, where the latter seems never to appear, and in Viburnum Lantanoides, where, according to Sanio, phellodermal cells are at any rate still absent in stems five years old. Many Coniferæ also appear to form no phelloderm, though this still requires more accurate investigation. In most woody plants phelloderm appears in the normal course of development, whether immediately after, or almost simultaneously with, the first cork-cells, or only in later stages of development, after the latter have already been produced in abundance.

The differences in these respects, which may be referred to in detail in Sanio, *l. c.*, are partly determined by the species, while within the same species individual variations occur, which often clearly depend on external causes. As regards the former, it is the rule for a number of investigated species, that at first only centripetal divisions and production of cork-cells take place, and only at a later period, often not before the second year, a layer of phelloderm is formed by a reciprocal division, which is immediately succeeded

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[1] Schacht, Lehrb. I. p. 287.

[2] Vöchting, Bau, &c. d. Melastomeen, p. 49.

[3] Vöchting, *l. c.*

again by those in centripetal order. The latter process may then be subsequently repeated from time to time. This is the case in most Pomaceæ, Virgilia, Solanum Dulcamara, Hamamelis, Platanus, and Acer campestre. In the majority of the forms investigated, however, the appearance of at least one layer of phelloderm immediately after the first divisions is the rule, and division thus takes place in the orders termed by Sanio centripetal-intermediate (Aronia rotundifolia, Fagus, and Rhamnus Frangula), centrifugal-intermediate, and centrifugal-reciprocal. The two latter orders of succession occur, for example, in Staphylea pinnata, and all the species enumerated on p. 548, after the mark ;—.

Sanio describes in Viburnum Opulus an exquisite example of individual variations. In summer the first layer of periderm is here formed in the centrifugal-reciprocal order, the reversal of the centrifugal succession taking place after 3–5 divisions. In internodes, which only develope their periderm later, in September, the reversal takes place more rapidly, immediately after the second division (centrifugal-intermediate order); those internodes, finally, which only begin to form cork late in autumn, show a purely centripetal succession. The relations which here manifestly exist between the change in the process of development and the action of external agents (warmth, light, &c.) may be recommended to more accurate physiological investigation. Various similar changes, which cannot always be brought into relation with external influences, are described by Sanio, *l. c.*

The number of the phellodermal layers, which arise in the structures under consideration, is in most species very small, in comparison with the cork-layers which appear in the same space of time. In each radial row only one or two phellodermal cells correspond to numerous cork-cells, even after several years; in periderms which grow for a very long time, e. g. Fagus, this relation constantly becomes more striking as time goes on; in a branch of this tree four years old Sanio figures two phellodermal layers to more than seven cork-layers, and found in branches twelve years old only two or three layers of phelloderm, while the number of the cork-layers, though not exactly stated, had certainly increased considerably.

Here also, however, numerous deviations from the usual rule occur, generally according to species and genera. In most investigated species of *Salix*, each initial epidermal cell produces in the first year *one* cork-cell externally, and *one* phellodermal cell internally; between the two there is a central meristematic cell, with its wall thickened on the outside, and immediately becoming cuticularised on the external thickened surface. In this central meristematic cell the same division and differentiation as in the initial epidermal cell is repeated in the second year, and the same process takes place in each succeeding year, starting from the meristematic cell for the time being, until the formation of bark begins at a later period. An abundant formation of phelloderm—six layers by the third year—was found by Sanio in *Quercus Suber*, where, however, the formation of cork-cells is also very abundant. *Canella* alba and *Cinnamodendron* corticosum may also be mentioned here; the thin old cortex of these plants, which is used commercially, shows (when not externally abraded), in so far as the structure can be recognised from the seriation of the elements in question, massive zones of phelloderm, which may be over twenty layers thick; these lie inside bulky layers of cork, and are separated from them by a layer of meristem. The elements of the phellodermal rows are almost cubical, and consist chiefly of stone-sclerenchyma, but with the latter thin-walled, unlignified cells, sometimes containing starch, sometimes clustered crystals, are intermixed in the most various ways. My material did not allow of a more accurate determination of the origin of these suberous and phellodermal structures; according to observations on single pieces of cortex their development in the deeper cortical layers is at any rate not improbable.

As is evident from the preceding statements, and from those in Sect. 24, the quantity of *cork-layers* originally formed, and of those produced anew by the meristem to replace the layers which peel off during the progress of growth in thickness, is

very unequal in the different cases. To these differences others are closely relate which affect the form of the cork-cells and the cohesion of the layers.

According to these differences two forms of the superficial formation of co may be distinguished, though they cannot be separated quite sharply: namel *suberous crusts* and *suberous integuments*. The former consist of numerous layers soft wide cork-cells, which alternate with thin flat-celled zones, marking the limits the annual production (p. 114). They constitute superficial masses, attaining thickness of several millimetres or centimetres, which are soft, and concentrical zoned internally; from their origin onwards they are provided with wing-lik projections and deep furrows, because the formation of cork is from the fir unequally abundant in alternate longitudinal bands; as growth in thickness go on they become widely and irregularly cracked. This is especially the case Quercus Suber and occidentalis, also Q. pseudosuber, climbing Aristolochiæ, e. A. cymbifera and A. biloba (cf. Fig. 219), the younger shoots of Acer campestr Liquidambar styraciflora, Ulmus suberos Euonymus europæus; species of Banks and Hakea (Mohl); further, in the abov mentioned cortex of Canella, the phelloderm covered externally by thick soft layers of cor

FIG. 219.—Aristolochia biloba; transverse section of the stem. *a* strongly developed cork with deep cracks (magnified about four times). From Schleiden, Grundz.

Suberous integuments, the periderm Mohl, consisting of flat cells only, or als of thin wide-celled layers alternating with th latter (e. g. Betula, Boswellia, &c., comp. Sec 24), form those smooth coverings of the corte which are present in the great majority woody plants. Their bulk in shoots of th same age is very various in different specie according to the amount of the annual nev formation and the extensibility of the walls of the cork-cells. All these co ditions may remain the same as long as the superficial periderm exists at all, they may change at various periods in the age of a shoot. These circumstanc determine the extremely various character of the surface in those woody plants whic persistently form periderm, to illustrate which some few examples must suffice here.

As already mentioned, many species of *Salix* (e. g. Salix alba) in their younger yea annually form a layer of cork-cells, all successive layers being of the characteristic stru ture described on p. 549; the outermost follow the growth in thickness by their extensio and finally they burst imperceptibly, and peel off, the cork-layer therefore remainin thin and smooth.

Fagus silvatica forms a highly extensible and firm suberous integument, which, from th first year onwards throughout life, consists of uniform flat cells with brown contents, an receives only a slight successive increment of growth from the meristem. The youn stem or branch has therefore a smooth brown surface. The external layers of th suberous integument burst imperceptibly, and wither, while their contents becom discoloured. Towards the tenth year of life[1] the process becomes more active, an begins to give the smooth surface that dull whitish colour by which it is permanent

[1] Hartig, Forstlich. Culturpfl. p. 177.

characterised throughout life (if rare exceptional cases, in which bark is formed later, be left out of consideration).

Similar conditions occur in other woody plants with a permanently smooth suberous integument, e. g. species of *Carpinus* and *Planera*. Others, as for example the species of Prunus, likewise form, so far as is known, only uniform, flat-celled integuments of cork, but the latter are thicker, and extremely tough, and long resist the action of the weather. In consequence of the latter properties the outer layers, when finally burst, adhere to the surface of the cortex as tough membranous flaps.

The shoots of *Corylus* Avellana form in the first year a suberous integument consisting of wide thin-walled cells. The latter soon bursts, and forms the yellowish gray, easily-peeled coating of the one-year-old shoots. Later on, firm, flat-celled, and soft wide-celled layers of cork (one or two strata of cells thick) are alternately formed; the latter burst readily, the firm ones peel off from them in shreds, which remain adhering to the shoots when the latter are several years old.

Betula alba forms from the first year onwards a firm suberous integument consisting of uniform flat cells with brown contents. The shoots therefore possess in the first instance a smooth brown surface. Later on, beginning at about the fifth year, wide-celled, thin-walled layers alternate with the flat-celled ones, the former being at first simple, but afterwards consisting of several or many strata of cells. In later years the brown mass of contents is absent, even in the newly-formed flat-celled layers, the entire suberous integument becoming colourless. The tearing of the thin-walled layers results in the peeling off of the corky integument.

The remarkably tough, leathery, thick suberous integuments of *Boswellia* papyrifera split into sheets owing to the tearing of the thin, brittle, silicified layers, which were described above in Sect. 74.

Sect. 176. A number of stems and branches of Dicotyledons, and almost all roots of Dicotyledons and Conifers, undergo a profound anatomical change on the formation of periderm, inasmuch as the latter takes place in the *interior*, at a considerable distance from the surface, and all parts lying outside the periderm, being cut off by the corky layer from the access of the sap, die away. The masses of tissue thus cut off are termed the *bark* (Mohl, *l. c.*).

The internal periderms arise round the whole member, by means of the process of development generally characteristic of peridermal formations, in a surface which is everywhere approximately equidistant from the centre, and which follows the periphery of the bast. Its transverse section, corresponding to that of the bast, is either circular, or indented opposite the medullary rays. According as the general surface of the member is similar or dissimilar to that of the bast, the peridermal layer therefore lies either at a constantly equal, or at a variously unequal distance from the former. Thus, for example, it surrounds the circular transverse section of the bast in Thuja and Juniperus as a ring, lying at a great distance from the surface opposite the corners of the branches, and only separated from it by a narrow zone of parenchyma between them. Between the corners or projections of the branches of Casuarina, it may even lie immediately below the epidermis.

With reference to its special position, it will be best to distinguish between stems, or their branches, and roots.

1. It has already been stated that in many stems of Leguminosæ the initial layer for the formation of periderm is the second or third layer of cortical cells from the outside. These cases effect the transition to those, which have to be considered here, with a more deeply situated initial layer.

The position of the latter, as is probable *a priori* from the occurrence of transitional forms, is not determinate in a sense generally applicable to all cases. It lies:—

(*a*) At a relatively great distance from the bast-layer; this is conspicuous in the case of Berberis vulgaris, where it borders immediately on the broad sclerenchymatous ring of the external cortex (p. 419), and is separated from the phloem-bundles by a broad zone of lacunar parenchyma containing chlorophyll. The same is the case in shrubby Papilionaceæ like Sarothamnus, Colutea, and Coronilla Emerus; also in Ginkgo; Caragana arborescens[1] and the stems of perennial Caryophyllaceæ (Dianthus, Silene spec.) have the cork-layer close inside the sclerenchymatous ring, which is separated from the bast by a zone of parenchyma. The formation of periderm in Casuarina and the Abietineæ, which, on account of some peculiarities, must be more minutely considered below, may also be placed in this category.

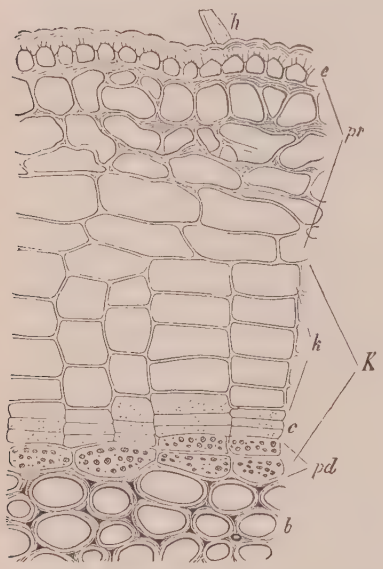

FIG. 220.—Transverse section through the surface of the cortex of a one-year-old branch of Ribes nigrum (500). *e* epidermis, *h* hair, *pr* dried-up and distorted parenchyma of the external cortex, *b* external region of the bast; *K* periderm, consisting of the suberous integument *k*, phelloderm containing chlorophyll *pd*, and the phellogenetic layer of meristem at *c*. From Sachs, Textbook.

(*b*) It lies near the external limit of the bast-layer, and in fact, in the absence of distinct fibrous bundles at the outer boundary of the phloem-region, in immediate contact with the latter: Lycium barbarum, Cobæa, Ribes (Fig. 220), Deutzia scabra, species of Lonicera, many Melastomaceæ (Melastoma Heteromallum, species of Lasiandra and Heterocentron[2]), Thuja, and Juniperus; Atragene and Clematis may also be mentioned here rather than in the category with bundles of bast-fibres. Where the latter are present, the phellogen either lies immediately outside them (Rubus idæus, according to Sanio), or close to their inner boundary (Punica, Spiræa opulifolia, Philadelphus, Melaleuca, and Vitis). In the Melastomaceæ mentioned, the initial layer borders directly on the endodermis which surrounds the bast. How far such a relation to a plerome-sheath occurs elsewhere, remains to be investigated.

The succession of the divisions is, in the cases belonging to this series investigated by Sanio, centrifugally reciprocal (Berberis, Caragana, Lycium, Deutzia, Lonicera, Philadelphus, Rubus, and Melaleuca); in the Melastomeæ and Casuarina it is centripetal. In the other cases mentioned the order of division has not been more minutely investigated.

Phelloderm is formed in Ribes, Lycium, Caragana, Deutzia, Lonicera, and Spiræa, and also, as it seems to me, in the Cupressineæ mentioned; in the re-

[1] Sanio, Stahl, *l. c.*

[2] Vöchting, *l. c.* p. 51.

maining cases it has not been found, or is not mentioned. The cork-cells form collectively thin integuments, consisting of a few layers. The extremely irregular arrangement, still requiring closer investigation, of the thin suberous integument of Cobæa is worthy of remark.

As regards the very various details of the first development of the periderm, and the structure of its mature parts, we must refer to the monographs. Here some special cases only may further be described as examples.

The above-mentioned *Cupressineæ*, and no doubt their similarly constructed allies also, have in the young internodes more or less broad, blunt projections of the external cortex, running down from the leaves, and traversed by vascular bundles or resin-passages (Juniperus), or both, which pass obliquely to the next leaf above. The outline of the bast, as seen in transverse section, is circular. The initial layer of the periderm passes close by the bast,—its position still requires more precise determination,—and is only a few layers of cells distant from the epidermis between the foliar projections, but is far removed from it opposite them; the whole of the projections, with their bundles and resin passages, are cut off by the layer of cork.

The *Abietineæ*, so far as is known, behave very variously as regards the first formation of periderm. Abies pectinata, as stated above, forms its periderm in the sub-epidermal layer of parenchyma. According to Mohl's statements[1], which however do not enter very minutely into this point, the same conditions may be assumed to exist in A. sibirica and Pinus Strobus. A contrast to these is presented by Larix europæa, where the parenchymatous foliar pulvini, which contain resin-canals, are thrown off by internal formation of periderm in the first year. Whether the periderm is also deeply-seated between the pulvini, or whether, as conjectured by Sanio, it is here immediately hypodermal, as in the furrows of Casuarina, is not known. Abies excelsa, Pinus silvestris and nigricans behave, according to Mohl, in a similar way to the Larch, as regards the first formation of periderm in the pulvini, with the sole difference that the periderm, especially in Pinus, is inserted less deeply and lies outside the resin-canals.

Casuarina[2] has large longitudinal projections, separated by narrow furrows, on the internodes of the branches. The approximately cylindrical bast is surrounded by a broad zone of parenchyma containing little chlorophyll, which in the furrows reaches to the epidermis, but in the projections is separated from the latter by the masses of tissue described already, through which runs the vascular bundle of the next segment of the leaf above, almost at the level of the base of the furrow.

The formation of periderm begins in the furrows, and in fact in the sub-epidermal layer of parenchyma. It is continued from each furrow in both directions, through a layer of the internal parenchyma directed towards the vascular bundle, and finally through a band of cells running transversely through the phloem of the bundle. Thus in the furrows the epidermis only is cut off by the peridermal layer, while between them this is the case with the whole of the foliar projections, including the external part of their vascular bundles.

2. Internal primary formation of periderm is a quite general rule in those *roots* which grow in thickness according to the Dicotyledonous type[3], and its initial layer is here always the pericambial or rhizogenetic layer of cells, which adjoins the endodermis on the inside. In the seedling it extends in many cases upwards from the root, through the hypocotyledonary stem. Its beginning coincides with that of the more abundant cambial growth in thickness, and through the joint

[1] Botan. Zeitg. 1859, p. 337. [2] Sanio, *l. c.*—Löw, *l. c.*; compare p. 256.
[3] Van Tieghem, Symmétrie de Struct., *l. c.*

action of the two processes the whole cortex lying outside the pericambium or endodermis is as a rule split, and thrown off, suffering immediate decay in the case of subterranean roots, while it adheres to parts above the ground in the form of flaps, which gradually dry up. In parts which swell quickly this is very conspicuously apparent; the separation of the flaps from one another often takes place exactly along those longitudinal lines in which the cambiogenetic growth in thickness is at first most vigorous, and consequently in those lying opposite the primary phloem-bands of the vascular bundle. As in diarch main roots the latter alternate with the cotyledons, in such cases a separation into two flaps occurs, each of which lies below a cotyledon, a phenomenon which has often been described in the case of plants forming tuberous roots which, together with the hypocotyledonary stem, swell rapidly; it was completely explained by Turpin in 1830[1]. Where the swelling is less rapid, the process under consideration, by which the usually relatively voluminous primary cortex is thrown off, often results in a diminution of the total thickness of the member, which is only compensated by later secondary growth; most roots of Dicotyledons and Gymnosperms are thinner at the beginning of the secondary growth than before, owing to the loss of the external cortex.

The commencement and progress of the cell-divisions in the periderm of roots, though it has not been investigated in all its details, yet corresponds, so far as is known, to the general rules for the formation of periderm. According to the data made known by Van Tieghem, their products are in all cases, including the Coniferæ, both phelloderm and layers of cork. The former constitutes an external layer of the parenchyma, and is always of relatively small bulk. The cork-cells generally form thin integuments, rarely (e.g. Pistacia Lentiscus) more bulky, cracked masses of cork. In the more or less fleshy roots of herbaceous plants, the continuous suberous integument is often extraordinarily thin, being reduced to one or two layers of cells. The peeling off and decay of the outermost layers, for the time being, are no doubt considerably accelerated in the case of subterranean roots by the nature of their surroundings.

In the roots of woody plants the general character of the suberous integument is similar to that of the stem. No minute investigations exist on the special differences which may occur between the two in the same plant. In many herbaceous plants the relatively great irregularity in the arrangement of the whole peridermal layer is conspicuous.

The cells of the endodermis, which are likewise wholly or partially suberised, often form the outermost stratum of the cork-layer, when the external cortex begins to be thrown off, and, on further growth, are the first to be thrown off themselves.

Sect. 177. *Repeated formation of internal periderms.* The first formation of periderm, whether it be internal or superficial, is in many woody plants the only one, and the periderm follows the growth in thickness of the parts enclosed by it: Fagus. The great majority of ligneous plants, however, form on stem and branches new internal periderms, after the first one, which arise successively in deeper layers of the cortex, and cut off successively deeper zones of tissue as dry bark. This process

[1] Turpin, Ann. Sci. Nat. 1 sér. tom. XXI. p. 298, pl. 5. Compare Botan. Zeitg. 1873, pp. 129, 297.

has also been observed in roots (e. g. Sassafras, Vitis, &c.), but always to a small extent, and in a manner not differing from the stems, so far as is known. More accurate investigations only exist as regards the latter.

In species the first periderm of which arises deep in the cortex (Lonicera, Vitis, Clematis, Cupressineæ, &c.) all the later ones assume the same arrangement as the first, and thus cut off in each case an annular layer of cortex, though this is not always quite complete and regular (*Ring-bark* of Hanstein). In species with a superficial primitive periderm, on the other hand, the successive internal layers arise in such a form, that they abut on the outermost layer of periderm for the time being, and cut off scale-like portions of the cortex (*Scale-bark*). The single scales have extremely various forms and dimensions even in the same individual. Their formation begins at points which are not morphologically determinate; the first scale is joined, at or below its edge, by the peridermal layer which cuts off a second scale, next the first, and belonging to the same cortical layer, and the same phenomenon extends round the surface of the stem without any perceptible regularity, cutting off the first cortical layer in scales, and then in the same way attacking a deeper one. The scales which succeed one another at different depths also differ among themselves in form and size; they do not fit one on another.

The characteristics of a bark depend, next to the arrangement of its parts as stated above, on the structure of the tissue which becomes dried up, and on that of the periderm, especially of its suberous layers. As regards the former, essential differences are due to the varying hardness and toughness of the desiccated layers of tissue, determined by the occurrence of fibrous and stone-sclerenchyma between the softer tissues, which on drying often become brittle and easily crumble. The thickness of the zone of tissue thrown off each time also has an influence, and is extremely various according to the special case, examples of which will be found in subsequent descriptions. In the cork-layers all the above-mentioned differences of structure occur, and according to their combinations, numerous peculiarities appear in the various species.

The difference in the cohesion of the membranes of the old cork-cells which undergo desiccation is of primary importance. If they are thin and not very tough, they must become torn, on the one hand by the progressive extension of the periphery of the stem, on the other hand by the shrivelling of the layers of tissue while drying. If a stratum of cork of this nature coats the inner surface of a dry layer of bark, the latter breaks off completely. The well-known scaly bark of the Planes is an exquisite example of this. The stratum of cork bordering a scale is only a few layers thick, and consists in its outer part, adjacent to the scale, of thin-walled, brittle cells, while the more internal ones have thick yellow walls, as mentioned in Sect. 24. The scale is released by the thin-walled zone becoming completely torn through, the thick-walled zone remains till the next following desquamation, as a fairly smooth covering of the living tissue. The surface of the cortex thus remains, on the whole, smooth, with only those flat inequalities which correspond to the outlines of the desquamating portions, and change from year to year. The case is similar in Taxus baccata, in the false quinine bark occurring as China bicolorata, and in the stem of Arbutus Andrachne, A. Unedo, and Salix amygdalina and its allies; Pyrus Malus may also be mentioned here. In the

younger stem and apical branches of Pinus silvestris and its allies, the cork layers which cut off the young thin scales of bark consist, on the outside and inside respectively, of a few-layered stratum of thin-walled, easily torn cells, while between them a stratum occurs which consists of one or two layers of sclerotic elements; this does not always extend to the edge of the thin-walled strata. When the latter become torn the whole bark peels away, and forms partly the somewhat thin scales of true bark, consisting of desiccated cortical tissue and adherent layers of cork, partly those tough feathery sheets, of the thickness of paper, which are the sclerotic, hard, persistent layers of the suberous zones.

The peeling annular bark of species of Melaleuca (especially M. styphelioides), Callistemon, Vitis, Clematis, &c., also, strictly speaking, belongs to this category. It is however held fast for a long time in the form of fibrous flaps adhering to the cortex, and hindered from falling off by the numerous strands of bast-fibres which belong to the cortical tissue in process of desiccation; they traverse and support each desquamated zone surrounding the periphery of the stem, as a strong network of fibres with pointed meshes.

In cases where the cohesion of the old suberous membranes is greater, the layers of bark succeeding one another from without inwards adhere more closely one to another, as a connected crust, which, as growth in thickness goes on, becomes more and more cracked externally, and gradually suffers decay. Woody plants with a thick, cracked, and rugged bark, such as Oaks, Birches, Poplars, most Willows, Robinia, &c., afford universally known examples of this phenomenon; the cortex of the old stem of Pinus sylvestris may also be expressly mentioned as an example, because the difference which it so conspicuously shows from that of young stems and branches depends principally, though not exclusively, on the different cohesion of the above-mentioned thin-walled layers of cork. The further differences consist in the structure of the desquamating layer of bast, which is no doubt altered by the extensive formation of phelloderm, and in other respects still requires further study.

A necessary direct connection between the direction of the cracks in the surface, and the form, size, &c., of the scales of bark cut off, does not exist, at least not in the typical cases belonging to this series. In those which are intermediate between the latter and the cases of complete desquamation, represented by the Plane, such a relation may occur.

Secondly, and independently of the cohesion of the membranes, the thickness and special structure of the entire suberous layer come under consideration, and in this respect essentially the same differences exist, as were stated above, with regard to the formation of cork in general, and to superficial periderms.

In most cases, no doubt, the layers of cork which cut off the bark are membranes, a few (not much more than ten) layers of cells in thickness; the cells themselves then either belong to the flat form, e. g. Platanus and Pinus sylvestris, or are wide and even radially elongated (e. g. Melaleuca), the successive layers being similar or dissimilar.

On the other hand, in many cases of repeated internal formation of periderm, cork is produced in large masses, forming thick strata, consisting of very many layers, and perceptible to the naked eye as broad zones. In these cases the cork no doubt always belongs to the wide-celled, thin-walled form, or consists of

the latter together with concentric zones of flat elements alternating with it. Examples of this are afforded by Acer campestre, with broad, soft zones of cork; by the older, bark-forming cortex of Betula alba, also with broad zones of cork, of similar structure to the white superficial periderm of younger stems, but firmer; but more especially by the Cork Oaks. The cortex of the stem of *Quercus pseudo-suber* is covered, in the thick pieces of the stem investigated, which was at least forty years old, by a crust of cork, attaining 2^{cm} in thickness, and cracked externally; it looks like bad bottle cork, and has the same structure as the latter, with reference to the cork-elements. It includes at various depths, numerous scattered isolated scales of desiccated cortical tissue, which are scarcely more than 2^{mm} thick, and 1^{cm} to about 6^{cm} broad and long. The oaks which yield true cork, especially *Q. Suber*, have, in the wild condition, the tendency to a similar formation of bark, but with a far more abundant production of cork. The latter indeed appears chiefly as superficial periderm (comp. p. 550); but it may also proceed, in the wholly intact tree, from internal, repeated periderms, and thus cut off narrow portions of cortex between broad zones of cork[1]. With the object of obtaining technically valuable cork, the tendency of the tree to the repeated internal formation of periderm is made use of artificially in the Cork Oaks and the Birch. The numerous misunderstandings regarding the modes of procedure and phenomena then taking place, some of which have re-appeared even in recent times, may justify a short account of the facts in this place, leaving purely technical matters untouched.

The intact *Cork Oak*[2] forms on stem and branches the superficial periderm above described, producing the thick mass of cork, which becomes cracked externally. Even on branches and stems many years old this form only is generally observed, covering the cortex, the whole of which remains alive, while the internal periderms just mentioned only occur exceptionally; this however may depend on the fact that old intact stems but seldom come under observation. In order to obtain cork for technical purposes, the almost useless, superficially-formed layer (called the male) is removed from the stem all round (démasclage); this is done carefully and smoothly, but not without everywhere injuring and exposing the living cortical tissue —in the best case at least the layer of phellogen and the phelloderm. While the cortical tissue begins to die off on the injured surface, a new periderm appears, one or two millimeters below the latter, around the entire stem; and its phellogen produces a new layer of cork, which cuts off the portion of cortex lying outside it. This periderm grows quicker than the external male cork, and is used technically as 'female cork.' The first peeling off of the male cork is undertaken when the tree is about fifteen years old. A serviceable female layer of cork is formed in about 10–12 years; a layer now before me, twelve years old, has, for example, an average thickness approaching 3^{cm}, without having undergone any further dressing. The female layer of cork, when sufficiently thick, is now peeled off like the male one, in order to be made use of, and is again replaced by the tree, in the way described above, by an internal formation of periderm. The same process may be repeated periodically, until the tree attains an age of about 150 years. If left to grow indefinitely, a female layer of cork may attain an immense thickness; I have a piece before me 17^{cm} thick, though of course of very bad quality.

A quite similar method to that used for obtaining oak-cork is employed in the northern

[1] Compare C. de Candolle, Mém. Soc. Phys. de Génève, XVI. p. 1 (1861), Taf. I. Fig. 2.

[2] C. de Candolle, *l. c.*—Von Mohl, Botan. Zeitg. 1848, p. 361.—See also Flückiger, Pharmacognosie, p. 334.

provinces of Russia for repeatedly obtaining the suberous integuments of Betula alba. In this tree also the layer of cork subsequently formed internally is distinguished from that first formed by its greater softness, which depends on the predominance of delicate, wide, cork-cells [1].

Sect. 178. If the woody plants investigated be compared, on the basis of the data given previously, and in Sects. 175–177, with reference to the occurrence and absence of the layers of periderm described, and the appearance and periodical changes of the latter according to the time, region, and individual, the following cases are found to occur.

1. Few Dicotyledonous woody plants, and no Gymnosperms, keep their epidermis, and are destitute of any formation of periderm throughout life, or during a considerable number of periods of growth. Cases belonging to this category have been mentioned at p. 535. Among woody plants with abundant growth in thickness Acer striatum is the most remarkable known case; in stems a foot thick, at least forty to fifty years old, I found the epidermis still for the most part preserved, with only isolated local spots of periderm, as to which it further remains doubtful whether their origin had not been caused by slight wounds.

2. The great majority of the *stems* in question form superficial periderm; a relatively small number of these (Negundo, Ilex, Sophora japonica, &c.) form periderm only in the second, or a still later period of vegetation of the shoot; it is formed in the great majority during the first period of vegetation, after the extension and primary differentiation of tissues is complete in the internode concerned; in our climate the formation usually begins between the end of May (Æsculus) and the end of July (Tilia). Late shoots may form periderm before extension is complete [2].

Many trees confine themselves to the formation of superficial periderm during life, or for many years. The periderm follows their growth in thickness. In consequence of this they have a smooth cortex, with a suberous integument, or a cracked covering of cork where the latter is massively developed (Quercus Suber). This condition is permanent through life in the common Beech, and for very many (nearly fifty) years at least in Abies pectinata, Carpinus, the Cork Oak, and many others.

This too, again, is an exception as compared with the majority of the cases. Much the greatest number of woody plants of this category form internal periderms later on in periodical repetition, and throw off the superficial periderm together with the successive external cortical zones, in the form of *scale-bark*.

As regards the age at which internal formation of periderm and desquamation of the bark begin, few very accurate statements belonging to this subject exist. In many trees it happens quite early; in Ulmus effusa as soon as the third or fourth period of vegetation of the shoot, in Robinia pseudacacia, according to Hartig, often even in the first. According to the same author [3] it begins in the native Oaks in the

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[1] Compare von Merklin, Mélanges Biolog. de l'Académie de St. Pétersbourg, IV. (1864), p. 563.

[2] Compare Sanio, *l. c.* pp. 41, 58.

[3] Compare the description of the trees mentioned in his Forstl. Culturpfl.

twenty-fifth to thirty-fifth year of life; in the Alders in the fifteenth to twentieth, the Limes in the tenth to twelfth, in Salix amygdalina in the eighth to tenth; in other Willows, with relatively abundant bark, earlier. In the Birch (B. alba), the formation of bark begins on the stems, from the fifth or sixth year of life onwards, starting at the base, and gradually advancing upwards, seldom to a greater height than four metres. Populus tremula keeps its smooth superficial periderm for many years; in P. nigra and pyramidalis it is soon thrown off by the formation of bark.

According to Mohl[1] the stem of Pinus sylvestris and nigricans begins the formation of its thick scale-bark in the eighth or tenth year.

3. A relatively small number of woody plants, mentioned above at p. 552, form their first periderm deep down in the cortex, and thus cast off the external layers of the latter at once. In the known cases this always happens during the first period of vegetation of the shoot, or at the limit between this and the second. In the further behaviour the following different phenomena then appear.

(*a*) After the formation of the first periderm the shoot remains covered by it; it follows the growth in thickness throughout life, or at least for years, and a renewed formation of internal periderm and bark only appears at a late period. In the stem of Cobæa scandens, after the external cortex has been cast off in the first year, and the bast-layer coated by an irregular periderm, no further internal formation of periderm has been observed. The latter occurs in Ribes (according to Hanstein, *l.c.*); also in Punica Granatum, where the one-year-old branch, after it has become coated with periderm, and has cast off the external cortex, as mentioned above, may grow for 10–20 years in thickness, before a new formation of bark (no doubt in the annular form) once more throws off a narrow cortical zone. Among Coniferous trees may here be mentioned Pinus sylvestris and nigricans, in which the casting-off of bark begins on the stem at the eighth to the tenth year; Larix, with a formation of scaly bark beginning approximately in the eighteenth year, and afterwards frequently repeated; and Abies excelsa, where this process begins about the twentieth year[2].

(*b*) The first annular internal formation of periderm is followed by that of successive new zones, of similar arrangement, at short intervals, which have not been more accurately determined, and without exact, or at any rate without exactly investigated, relations to the annual secondary growth of the bast. So in the majority of the above-mentioned woody plants with annular bark, e.g. Melaleuca, Callistemon, Cupressineæ, &c., the cortex of which becomes covered within a few years by several layers of bark.

(*c*) In every period of vegetation succeeding the first a new zone of bast is produced, and at the end of the period the whole zone belonging to the previous year is cast off by formation of periderm: Vitis, Clematis, Atragene and Caprifolium.

4. So far as is known, the woody plants investigated either show the same behaviour in all individuals, or hereditary individual differences. Examples of the latter have been mentioned above in the case of the Stone Beech, and the Cork Oaks which form bark; the variety of Ulmus effusa, known as the Cork Elm, with large wing-like outgrowths of cork, on the surface of the first periderm of young shoots, which is cast off about in the sixth year, may also be mentioned here.

[1] Botan. Zeitg. 1859, p. 338.

[2] Von Mohl, *l.c.*

5. The phenomena described usually extend uniformly over the whole of the stem and its branches; examples, however, occur of differences in the formation of periderm in zones at different heights. This is the case in Pinus sylvestris (p. 556), a tree which is distinguished by the thick bark on the lower stem, and the fine peeling bark on its apex and branches, from its allies, e.g. P. Laricio, in which the thick bark extends to the apex. According to Hartig this is also the case in the Birch, in which the higher portions of the stem, and the branches, independently of their age, constantly remain covered by superficial periderm only.

Sect. 179. *Lenticels*[1]. In most woody plants which form periderm the uniform peridermal integuments hitherto described are interrupted at definite points, to be more exactly indicated below, by bodies which are as it were inserted in them and belong to them, to which De Candolle gave the name of *Lenticels*, and Du Petit-Thouars the more descriptive one of *cortical pores*. Only in relatively few woody plants, provided with a regularly repeated annular formation of bark, have lenticels as yet been sought in vain: Vitis vinifera, Lonicera italica, L. periclymenum, Tecoma

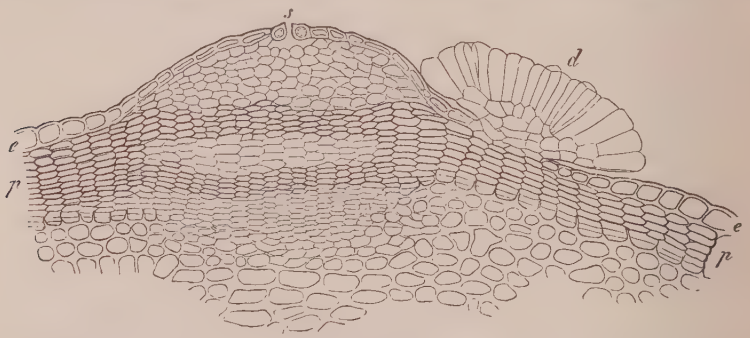

Fig. 221.—Transverse section through the cortical surface of a shoot of Betula alba one year old (145). *e*, *e* epidermis, *s* stoma, *d* glandular scale, *p*—*p* superficial periderm, with a lenticel interpolated below the stoma. In the lenticel two firmer, denser tangential bands are visible; but the narrow intercellular spaces containing air are left undrawn in the whole of the lower part, on account of the low magnifying power.

radicans, species of Clematis, Philadelphus and Deutzia, and Rubus odoratus, while, on the other hand, they appear in other plants, which are nearly related systematically to those mentioned, or agree with them in growth, habit, and formation of bark; as in those Loniceras which are not climbing, Solanum Dulcamara with annular bark, Ampelopsis, Periploca, Wistaria sinensis, &c.

Those species which form lenticels anywhere, have them both on the stem and its branches, and on the root.

According to its structure (comp. Fig. 221, and Figs. 222 and 223 below), the lenticel may in most cases be appropriately termed a local, bi-convex swelling of the periderm, often projecting above the surface as well as internally; it is distinguished from the rest of the layer by the presence of narrow intercellular spaces

[1] Von Mohl, Unters. üb. d. Lenticellen, Verm. Schriften, p. 233; also p. 229.—A. Trécul, Comptes Rendus, tom. 73, p. 15.—E. Stahl. Entwicklg. u. Anatomie d. Lenticellen, Diss. and Botan. Zeitg. 1873.—G. Haberlandt, Beitr. z. Kenntn. d. Lenticellen, Wiener Acad. Sitzgsber. Bd. 72 (1875). [Also Kreuz, Entw. d. Lenticellen von Ampelopsis hederacea, Wiener Acad. Sitzgsber. Bd. LXXXIII. 1881; and Potonié, Lenticellen d. Marattiaceen. *Ref.* Bot. Centralbl. 1881, Bd. 8, p. 70.]

containing air between the rounded edges of its suberous, phellodermal and meristematic cells. By means of these spaces, the intercellular air-spaces of the cortical parenchyma are in open communication with the external air at the time of active vegetation, as may be proved experimentally; during the resting period of vegetation this connection may be interrupted by an integument of ordinary cork consisting of but few layers.

In the fully developed lenticel minute investigation shows a phellogenetic layer of meristem, connected with that of the adjoining periderm, and the former, in so far as it belongs to the lenticel, either lies in the same surface as the surrounding portion of the layer, or it bulges out towards the inside, or more rarely towards the outside (e. g. old lenticels of Ginkgo). The cells of the lenticel are either approximately similar in form to those of the surrounding periderm, or, not uncommonly they are narrower in the tangential direction. After its first formation the meristematic layer of the lenticels behaves similarly to the rest of the phellogenetic meristem as regards its production of tissue. Like the latter it always forms phelloderm internally, and in fact in abundance; the latter may be as much as forty cells in thickness in each radial row, e. g. in old lenticels of Ginkgo. On the outer surface the elements termed by Stahl the *complementary cells* of the lenticel are first and principally formed in the same manner as cork-cells, and like the latter are arranged in radial rows; they are approximately isodiametric cells, similar to the cork-cells in form, but varying according to the species, with a thin colourless membrane, which for a long time shows the cellulose-reaction, and only at a later time becomes brown (suberized?), and does not otherwise present any peculiarities of structure; they have a persistent, colourless, protoplasmic layer lining the wall, and this layer contains a nucleus and often small quantities of starch, and encloses cell-sap which is also colourless. A remarkable peculiarity of the complementary cells, especially of the younger ones, which has not been sufficiently investigated, is their hygroscopicity, if the expression be allowed, i. e. their tendency to take up water and thus to swell. The often conspicuous, puffy swelling of the lenticels on the living tree in wet weather depends on this property, and it is further known [1], that after dipping in water the younger internal tissue swells up to a white mass, which exudes from the bursting surrounding tissue, becomes irregularly split up into tatters and fragments, and finally breaks up on the surface into its separate rounded cells. During this process a considerable, permanent increase in size of the cells takes place, at least in many cases, especially in the radial direction; e. g. the roundish isodiametric complementary cells of Sambucus nigra become extended into radially placed cylinders, which may become four times as long as broad.

In the cases of the formation of lenticels below stomata, to be more exactly described below, the first formed, most superficial complementary cells, differ from those described in the fact that they are arranged irregularly, and not in radial rows.

The complementary cells, like the phelloderm belonging to the lenticel, are rounded at their radial angles, and between the latter interstices containing air exist, which effect the above-mentioned communication of the cortical intercellular spaces with the surrounding air. The rounding is either confined to the narrow corners,

[1] De Candolle, Ann. Sci. Nat. 1826, VII. p. 5.—Von Mohl, Flora, 1832, Verm. Schriften, p. 229. —Unger, Flora, 1836, p. 577, &c.

the other surfaces of the wall being flat and in close connection with one another (e. g. Ginkgo, Sambucus and Lonicera); or the walls are rounded off on the greater part of their surface, and the cells are therefore only in slight connection, forming, especially when dry, a loose, powdery mass, e.g. Prunus avium, Pyrus malus, Robinia, Betula, Æsculus, and Gleditschia. In the latter case the mass of complementary cells is held together, owing to the fact that some layers of flat cells, firmly but not uninterruptedly connected among themselves and with the adjoining loose ones, are always formed alternately with some loose layers of complementary cells.

In the complementary mass of Quercus Suber, which is also loose and powdery, I did not find this arrangement; the cohesion is here due to the fact that the whole lenticel is enclosed in the tough, firm mass of cork, and thus protected from falling to pieces, as will appear still more clearly below.

The firmer layers in the loose lenticels appear independently of the limits between the periods of vegetation; e. g. Fig. 221 shows two of them in a lenticel taken from a this year's shoot of the Birch on the 5th of June. In older lenticels, however, even in those filled with dense tissue, the formation of an uninterrupted layer of cork over their whole surface occurs in many trees at the close of each period of growth; at the beginning of the next period complementary cells are then again added by the meristematic layer. Where such a layer of cork appears at the close of each period of vegetation (e. g. Ginkgo) it marks the limits of the annual zones of growth.

The uninterrupted layers of cork serve to shut off the internal intercellular air-spaces; the former therefore constitute the 'closing layers.' The closure is, however, temporary, as the successive layers of cork are again burst by the subsequent formation of complementary cells.

In trees which form an autumnal closing-layer, the latter is, according to Stahl, already present before the time of the fall of the leaf. The renewed formation of complementary cells below it begins with the next period of growth, but need not immediately result in rupture and the opening of aerial communication, as this obviously depends on the relation existing between the pressure exercised by the new formation and the resistance offered by the closing layer. As a matter of fact, judging from Haberlandt's experiments[1], this usually begins after the trees have completely expanded their leaves, or even after the close of the flowering season in those in which the flowers appear later than the leaves, although, according to the author's own judgment, no certain conclusion can be drawn from these experiments alone, but more accurate results must be sought by means of anatomical investigation.

The outermost layers of the lenticel, for the time being, undergo, in proportion to the progress of growth in thickness and phellogenetic new production, the same passive changes as the layers of cork, namely desiccation and gradual decay.

The productiveness of the phellogenetic layer in a lenticel is, as a rule, especially in the centrifugal direction (centripetal with reference to the succession of the dividing walls), greater than outside the lenticels; the latter therefore project as convex bodies above the surrounding peridermal surface. Only in those trees, which like Ulmus, Liquidambar, Euonymus europæus, and Acer campestre, form wing-like,

[1] *l. c.* p. 16.

projecting outgrowths of cork, does the converse case in a certain sense appear, the lenticels lying in the depressions between the wings. In the case of the thick corky layers of Quercus Suber also, the inequalities of which are principally due to mechanical cracking, the lenticels do not appear above the surface; they traverse the layers in the form of radial, irregularly constricted cylindrical columns, consisting of a loose mass of complementary-cells which become brown on drying, and extend from the withering surface to the phellogen; they are known to everybody who has seen a cork stopper as the brown pulverulent stripes, running at right angles to the annual layers.

A lenticel, belonging to a persistent periderm which increases successively in circumference with the growth in thickness of the shoot, behaves differently according to the species, as regards its own growth in breadth. In numerous kinds of trees, as Prunus avium, Betula, Abies pectinata, and Tamarix indica, every lenticel apparently increases in breadth in about the same proportion as the circumference of the shoot. On old stems or branches the lenticels appear as large, transverse segments of rings. Although accurate measurements are wanting it may yet be asserted of these cases with approximate exactness, that the portion of phellogen belonging to the lenticel follows the dilatational growth in the same way as is known to occur in the rest of the periderm, and persistently forms lenticel-tissue.

In other cases, e. g. Fraxinus excelsior, F. Ornus, Ailantus, and Quercus Suber, the lenticels show little or no increase of breadth, or even show a decrease as they become older. In a third series, finally, e. g. Pyrus Malus, Rhamnus Frangula, Broussonetia, and Tsuga canadensis, as well as Quercus Suber, a lenticel may be divided up into several smaller ones by dense periderm. The latter case can only arise owing to the fact that at certain points in the phellogen of the lenticel, cork instead of complementary tissue is formed from a definite point of time onwards (no doubt from the date of the autumnal formation of the cork-layer). The same process must go on progressively from the periphery towards the centre of the lenticel, when the latter diminishes in its superficial extent. Where the latter remains the same or increases slightly, it is doubtful whether the process just mentioned takes place in proportion to the dilatation of the phellogen of the lenticel; or whether, as is less probable, the latter takes no part in the general dilatation of the cortex, or a lesser part than the periderm outside the lenticel.

According to what has been stated, the absolute size of the lenticel may change considerably with age, in the same individual, the transverse diameter attaining the length of 1^{cm} and more, in lenticels which participate in the growth for a very long time. The original superficial size, which remains unchanged in those growing but little in breadth, may be stated at about 1^{mm}. In periderms which are quickly cast off, e. g. that of the Plane, considerably smaller lenticels occur, which can scarcely be clearly distinguished with the naked eye.

The *origin* of the lenticels shows differences respecting the region and mode of their formation, according to the position of the periderm to which they belong.

Where the seat of the first formation of periderm is the epidermis, or the subepidermal layer of parenchyma, or, as in the above-mentioned Leguminosæ, a slightly deeper layer, the lenticels arise *below the stomata*, namely one under each stoma when the latter are not very numerous and are uniformly distributed, e. g. Sambucus nigra,

Prunus Cerasus, Ligustrum vulgare, Syringa persica, Salix fragilis, Rhus typhinum, Fraxinus Ornus, Robinia pseudacacia, and many others;—or, where the stomata are grouped together, one lenticel is formed under each group, e. g. species of Populus, Juglans regia, and Hedera Regnoriana; the stoma under which the lenticel originates lies over the middle of the latter at a later stage of development, while other neighbouring ones may lie in the periphery, e. g. Euonymus europæus, Persica vulgaris, and Cornus sanguinea.

Even where the stomata are less numerous, some of them may remain without any share in the formation of lenticels, as is especially conspicuous in the horizontal shoots to be described below, in which the number of lenticels on the upper side is smaller than that on the lower side. In the investigated cases the stomata are here equally numerous on both sides, and on the upper side at least are always more numerous on the same area than the lenticels.

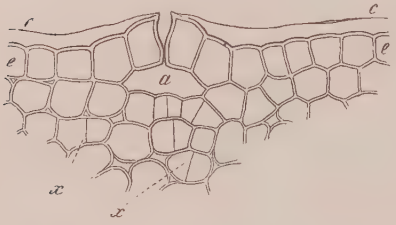

FIG. 222.—Transverse section through a young internode of a branch of Betula alba (375). *e*—*e* epidermis; *a* respiratory cavity under a stoma; *c* the cuticle, which is separated from *e* as far as the entrance of the pore by a layer of secretion (removed by alcohol). At *x* the first beginnings of the divisions which give rise to the complementary tissue.

The formation of lenticels below stomata begins with the growth and divisions of the parenchymatous cells lying in this position. (Figs. 222 and 223, comp. also Fig. 221, p. 560). The divisions at first take place variously in different directions. Their products, and also no doubt the cells which have not yet divided, grow chiefly in the direction at right

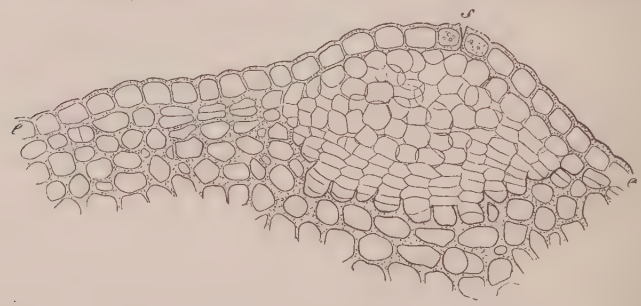

FIG. 223.—Transverse section through a lenticel of Betula alba; older stage than Fig. 222 (about 280). *e* epidermis, *s* stoma, under the latter the complementary tissue of the lenticel; inside this is its phellogenetic meristem. At the edge of the lenticel the tangential divisions in the hypodermal parenchyma which give rise to the superficial periderm are beginning on both sides.

angles to the epidermis; their angles become rounded, the chlorophyll originally contained in them disappears, and the cells acquire the properties of delicate colourless complementary cells. Similar changes now extend further in area and depth from the original point of departure. As this goes on the further dividing walls soon assume a more regular and uniform tangential position, in such a manner that the above-mentioned phellogenetic layer of meristem, which is usually concave towards the inside, finally appears. The mass of complementary cells lying outside this, in which the divisions soon cease, becomes more and more driven towards the outside, in conse-

quence of its own growth, and of constant additions from the phellogen; it first bulges out the epidermis, and then breaks through it by a longitudinal crack passing through the stoma, or through one of the numerous stomata, and then protrudes through the gap. The complementary cells coming out through the crack, which is constantly opening wider, then dry up, together with the shreds of epidermis adhering to them; they form those elements of the complementary mass which were mentioned above as not being radially arranged, and as peculiar to stomatal lenticels.

The beginning of the formation of lenticels takes place as a rule on the young shoot at an early period, before longitudinal extension is complete, and before the formation of other periderm. Indeed the latter as a rule starts from the edges of the lenticels, as soon as the phellogenetic layer is formed in the latter, and is continued thence over the surface of the shoot. Exceptions to this rule are rare, and apparently peculiar to individuals[1]. It is true that the two processes often follow one another immediately, so that the appearance of periderm and lenticels may be spoken of as simultaneous, without any great error. In shoots with a long-lived epidermis on the other hand (Sophora japonica, Rosa canina, Negundo, and Acer striatum), the lenticels already appear in the first year, and thus long before the further extension of the periderm.

It is obvious that according to the epidermal or sub-epidermal origin of the periderm, special differences must occur with reference to the conditions described, especially as regards the connection of the segments of the phellogen with one another. For these Stahl's work may be referred to.

In the superficial periderms, *all original lenticels*, so far as is known, are formed below stomata in the manner described.

Secondly, the formation of lenticels occurs *independently of stomata*, on periderms either when first developing, or in older stages, owing, as it may be shortly expressed, to the fact that the phellogenetic layer of meristem forms, on limited areas, lenticel-tissue instead of ordinary periderm. If this begins after layers of cork are already present, the latter are burst by the growing lenticel. A more minute description of these processes is superfluous after what has been stated above; for some special cases, and also for the peculiar formation of lenticels on the sites of the insertion of the leaves in Abies pectinata, a case which does not strictly belong to this category, reference may be made once more to Stahl's work.

Lenticels independent of stomata arise on the internal periderms, both on those first formed and on the succeeding ones, simultaneously with the origin of the rest of the peridermal layer (with the obvious exception of plants wholly destitute of lenticels).

According to Stahl's observation on Pyrus Malus, and Haberlandt's enumerations to be mentioned below, they may also be successively formed anew, between the pre-existing ones, on older periderms which have been growing for some time, whether these be superficial, or of endogenous origin.

The latter new formations increase the number of lenticels on those periderms which follow the dilatation. Those appearing on successive periderms replace those lenticels which are lost when the bark is separated. If the bark is thrown off in scales,

[1] See Stahl, *l. c.* p. 23.

as in Platanus and Pyrus Malus, the new ones appear on the surface laid bare by its removal. In trees with an adherent, longitudinally cracked bark, as Robinia, Prunus domestica, species of Populus, and Ginkgo, the living lenticels lie at the bottom of the longitudinal furrows. The first cortical cracks pass through the first-formed lenticels themselves, and give them the position indicated. New ones then arise in the peridermal layers which are successively laid bare at the bottom of the furrow, by the further extension of the crack.

According to the few existing enumerations, and judging from appearances, the number of the lenticels occurring on the same transverse portion constantly increases with the dilatation, at least in many trees; and probably to a greater extent, the smaller the dilatational growth of the individual lenticel.

As follows from the facts discussed above, the distribution of the lenticels on a shoot is in general determined by that of the stomata, by the structure of the older cortical surface, the form of the bark, &c. An additional phenomenon, independent of all these relations, further appears, namely, that while the distribution is uniform all round on upright shoots, in those growing horizontally the upper side has fewer lenticels than the lower side. The amount of difference between the two sides varies, according to the species, and according to the age of the shoots of a tree; in the latter respect in such a manner that it is greatest in young stages, and becomes more and more equalised as growth in thickness proceeds. Of the numbers found by Haberlandt for this relation, in several species of tree (species of Gleditschia, Tilia, and Ulmus campestris), some may be given here, which also illustrate the successive increase in the total number of the lenticels. The number on the upper side is printed as the numerator, that on the lower side as the denominator of a fraction.

Piece of branch, 20 cm long, of—

	1st year.	*3–5th year.*	*10–15th year.*
Gleditschia triacanthos:	$\frac{73}{210}$;	$\frac{110}{241}$;	$\frac{150}{290}$.
Ulmus campestris:	$\frac{55}{70}$;	$\frac{66}{78}$;	$\frac{95}{96}$.

CHAPTER XVI.

ANOMALOUS THICKENING IN DICOTYLEDONS AND GYMNOSPERMS.

Sect. 180. The secondary growth in thickness of stem and root differs in a number of Dicotyledons and Gymnosperms from that which is called normal because of its occurrence in the large majority of these plants; it is therefore called anomalous in the cases in question.

In the first place, we may range among anomalous forms those not uncommon cases, in which by reason of strongly eccentric growth of the xylem, while the growth in thickness of the surrounding cortex is almost uniform, the stem or root attain forms, which differ greatly from the ordinary conical or cylindrical form; but in which the other relations are normal. An exquisite example of this series is seen in the upright stem of Heritiera Fomes, described by Schacht[1], which, as far as may be judged from the description, grows at first in a manner in other respects normal, and uniformly all round, but later grows in thickness more especially at two opposite corners, so that it attains the form of a board, e. g. $1\frac{1}{2}$ ft. broad, and only 1 in. thick. Such phenomena appear in very striking form in climbing stems: species of Cissus, and Piper with strap-shaped stems[2]; Cassia quinquangulata[3] with five or more marked prominences, as seen in transverse section, each of these being opposite to one of the orthostichies of leaves; Lantana spec.[4] with four longitudinal prominences separated by deep furrows, and alternating regularly with the leaf-insertions, &c. In the above-named climbers there often appears a splitting of the whole stem at the furrows when it grows old. Again, allied but less regular inequalities occur not unfrequently in roots, and are characteristic, e. g. in those of Ononis spinosa described by Wigand[5]. All these appearances, considered anatomically, are nothing more than extreme instances of the widespread phenomenon of unequal eccentric development of the woody layers, which appear as specific peculiarities in the examples cited, while in other plants they may appear as phenomena peculiar to the individual, or induced by definite physiological causes. They may therefore be excluded from the subject now under consideration, reference being made to Sects. 138 and 140.

Sect. 181. A special anatomical treatment is, however, demanded by those

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[1] Lehrb. I. p. 344.
[2] Crüger, Botan. Zeitg. 1850, p. 121.
[3] Ibid. 1851, p. 469.
[4] Fr. Müller, Botan. Zeitg. 1866.
[5] Flora, 1856, p. 673.

anomalies of growth, which differ from normal cases in having some other arrangement of the initial layers which maintain growth, or some other distribution of the tissues, or in showing special phenomena of dilatation. It must be maintained from the first that even the anomalies to be described are derived from ordinary initial structures, which are usually formed according to the normal Dicotyledonous type; that in their case also we have to do with a further formation of secondary wood and secondary bast, which are derived from the same kinds of tissue as the normal formations; that their formation arises from secondary meristems and cambial layers, which, when present, behave fundamentally like, or very similarly to such normal tissues; and that, finally, the phenomena accompanying an increase by cambium, such as dilatation, formation of periderm, &c., also in themselves resemble those of normal examples. Hence also the same terms will be used, and in the same sense as in the foregoing paragraphs, except when special modifications are described by special terms.

The relations now under consideration differ from one another and from normal cases, both qualitatively and quantitatively, to a very variable degree, and are connected one with another, and with normal cases by various intermediate forms. If the latter be neglected, we have to deal with the following main phenomena.

1. Anomalous distribution of the tissues in zones of wood and bast, with normally derived, normally arranged, and permanently active normal cambium: Sects. 182–186.

2. Abnormal formation and arrangement of cambium, wood, and bast:—

(*a*) Besides the normal cambial ring a second appears, concentric with the first, at the inner limit of the ring of wood; Sect. 187.

(*b*) In place of the one normal cambial ring in the ring of bundles, there appear round the primary vascular bundles several separate cambiums side by side, either one round each vascular bundle, or one round each group of vascular bundles. Their position between the xylem and phloem of the bundle or bundles, and the arrangement of the secondary products of wood and bast relatively to the latter, resembles that in normal cases, Sects. 188, 189: rarely it is inverted, Sect. 190. Their productiveness is (compared with *c*) permanent. To distinguish them from the normal *general* cambiums they may be called *partial*, and the rings or zones of secondary growth derived from them *partial thickening-*, *wood-*, or *bast-rings* in contrast to the normal general ring. For shortness' sake, the woody ring is often simply spoken of when the whole ring is meant.

(*c*) *Renewed thickening zones.* The increase in thickness begins normally, then stops, and is continued by a new cambial zone, which is formed from secondary meristem in the parenchyma outside the first, and this, as well as an unlimited number of successive ones, may behave like the first, and like it be replaced by a fresh one. The successive zones, or cambial layers are nearly concentric, and arise in centrifugal order; their arrangement and productiveness are normal, as long as they continue: Sect. 191.

(*d*) *Extrafascicular cambium.* The cambial zone does not, as in normal cases, pass *through* the primary bundle-ring, but lies entirely *outside* it: the arrangement of the products of its activity differs from the normal: Sects. 192 and 196.

3. Abnormal dilatation of the internal old parenchyma belonging to the xylem,

usually connected with the appearance of new zones of *intercalary* wood, bast, and cambium derived from secondary meristem: Sects. 193, 194.

All these chief phenomena often show not only reciprocal approaches to one another, but often occur variously combined. The following description of concrete instances is arranged as nearly as may be according to the above heads, but cannot be classified exactly in that way, without relinquishing all clearness, and incurring endless repetition. The paragraphs specified under the single heads usually indicate those points only where the *most important* examples of them are to be found.

The consequences of increase in thickness as they affect the changes of the peripheral parts, dilatation, distortions, secondary metamorphoses in the cortex, and formations of periderm, are in general the same, and varied in the same manner in anomalous stems as in normal secondary thickening. They have been but little investigated in detail. They will therefore be only shortly noticed as opportunity offers in the following description.

Where cambium and bundles of wood and bast develope from secondary meristem, the latter always arises by division of parenchymatous cells, which are as usual for the most part relatively short, while the above-named tissues are composed of elongated elements. Those secondary formations must therefore induce distortion and displacement of the tissues present. With the exception of the one case, to be noticed below, of Cocculus palmatus, investigated and discussed by Radlkofer, Nägeli, and Eichler, no exact investigation has been made of these phenomena.

As is the case with almost all anatomical peculiarities the anomalies of secondary thickening also are in part evident phenomena of adaptation, and may in part even be explained directly as the outcome of mechanical causes; they are in part unexplained anatomical characters, which must be regarded as inherited. To the first category belong the anomalies of twining and climbing liane-stems from the most different families, whose non-climbing congeners have normal growth, as in the Bignoniaceæ, Sapindaceæ, Leguminosæ, Malpighiaceæ, and others to be named below. The lianes from certain families, especially the Sapindaceæ, or at least the majority of them, show very special peculiarities. On the other hand, a remarkable uniformity is often seen between those belonging to the most different families, as e. g. Menispermum and Gnetum, Bignonia and some Apocynaceæ, &c. To the second category of unexplained anatomical characters belong the phenomena to be described in the Chenopodiaceæ and their allies, in Strychnos, Avicennia, &c. It is sufficient to refer shortly to this, and to dispense with further observations, till exact investigations of individual cases have been published.

Sect. 182. As the first and simplest instance of *anomalous distribution of tissues where the cambium is normal* may be mentioned the case, in which the production of wood alongside of the latter is unequal in successive longitudinal bands, while the production of bast is more active opposite those bands where the development of wood is less. The wood, therefore, when considered separately, appears excentrically unequal in some definite form, or furrowed, in transverse section notched and lobed. The eccentricity is, however, equalised, and the furrows filled up by correspondingly large and specially formed masses of bast, and the whole form of the stem or root differs from that of the wood. Leaving cases of very slight inequality out of account,

the root of *Polygala Senega*[1] belongs to this series: here, as a rule, the wood grows strongly in thickness only in one approximate longitudinal half, the bast in the other. The former, as seen in transverse section, attains the form of a half-circle with the periphery turned towards its stronger growing side, or of a circle with a broad piece cut out of it on the weaker side. The transverse section of the bast appears as a narrow segment of a ring surrounding the more strongly grown half of the wood, on the other side as a large segment of an ellipse. In the dried root the stronger band of bast projects as the well-known keel.

Sect. 183. The inequalities in question appear in much more characteristic form in the stems of lianes with deeply grooved wood, and with bast-plates which project into the grooves: Bignoniaceæ, Phytocrene, and others to be named below.

In the climbing *Bignoniaceæ*[2], Figs. 224–226, the secondary growth of wood and bast is derived from a normal ring of cambium, and begins with the formation of a zone of wood and bast, of normal structure and equal thickness all round,

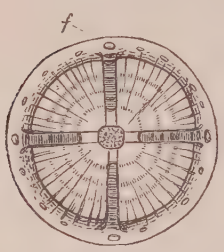

Fig. 224.

Fig. 225.

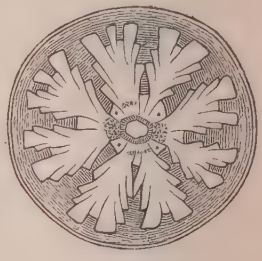

Fig. 226.

Fig. 224.—Anisostichus capreolata Bur. Transverse section through a four years' old branch, × 3. The annual rings and medullary rays are represented in the wood by radial bands, the bast-layer and bast-plates by concentric lines. The elongated figures in the peripheral cortex and the dark lines in the latter and in the four plates represent the fibrous bundles; *f* the four larger ones. The pith is dotted.

Fig. 225.—Transverse section through a non-identified Bignoniaceous stem (Pleonotoma?), from Schleiden, Grundz.; nat. size.

Fig. 226.—Melloa populifolia Bur. (Bignonia No. 17, Fr. Müller, Botan. Zeitg. 1866). Transverse section through a branch, × 2. Bast and bast-plates shaded, wood left white. The four first bands of wood, which have remained behind, marked thus (·); medullary sheath shaded radially, pith white. The dotted parts round the medullary sheath are large islands of parenchyma, the subsequent dilatation of which splits up and bursts the wood.

i. e. like a ring. The latter is limited from the primary outer cortex by an interrupted zone of fibrous bundles. In each internode there are four bundles of this zone (*f*), which are from the first larger than the rest. They lie always, according to Crüger, in four planes, which alternate regularly with the orthostichies of leaves, and are perpendicular with reference to the straight internode: in transverse section they are arranged crosswise.

At the beginning of the secondary growth in thickness, the increase of the wood in the longitudinal bands opposite the four large crosswise fibrous bundles is left

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[1] Walpers, Botan. Zeitg. 1851, p. 297; Wigand, in Flora, *l. c.*; Figures in Wigand, Pharmacognosie, and Berg. Botan. Zeitg. 1857, Taf. I; Atlas, Taf. VIII.

[2] Gaudichaud, Recherches, &c., sur l'organographie, &c., des végétaux (Mém. présentées à l'Acad. des Sciences, tom. VIII), Paris, 1841; Idem in Archives de Botanique, II. (1833).—A. de Jussieu, Monogr. des Malpighiacées; Archives du Muséum, tom. III. (1843).—Mettenius in Linnæa, Bd. 19 (1847).—Schleiden, Grundzüge, 3 Aufl. II. 165.—Crüger, Botan. Zeitg. 1850, p. 101.—v. Mohl. Botan. Zeitg. 1855, p. 875.—Bureau, Monogr. des Bignoniacées, Paris, 1864, p. 120; Id. in Bullet. Soc. Bot. de France, 1872, p. 14.—F. Müller, Botan. Zeitg. 1866, p. 65. [Westermaier u. Ambronn, Lebensweise u. Struktur d. Schling—u. Kletterpflanzen. Flora, 1881.]

behind by that of the rest of the circumference, while the converse holds in the production of secondary bast. While in other respects the wood increases as usual among the woody Dicotyledons, and remains surrounded by a relatively narrow layer of bast, it first appears depressed in the four longitudinal bands indicated, and is soon interrupted by furrows limited by flat lateral surfaces, which increase in depth as the thickening proceeds: the wood thus becomes four-lobed in transverse section: the groove is, however, exactly filled up by a bast-plate which runs out externally into the original bast, so that the cylindrical or ribbed surface of the stem suffers no important change of form through the unequal growth of the wood. The cambial zone surrounds, on the one hand, the four prominent portions of the wood as far as the margins of the bast-plates, and on the other hand, the outer surface of the four bands of wood of which the growth is suppressed: it forms at both points both wood and bast, but in unequal quantity as described. On the lateral surfaces of the bast-plates, from the margins to the inner surfaces of the furrows, it is interrupted; as soon as the inflexion of the wood begins, the cells at the margins of the grooves lose their cambial properties, and assume those of parenchyma of the medullary rays. At each margin of each of the eight sections of the cambial zone thus separated, the cells immediately adjoining it form henceforth only parenchyma of medullary rays; those of the margin of the projecting portions of wood form especially cells of medullary rays of the xylem in centrifugal succession, those at the base of the groove forming cells of the bast rays in centripetal succession.

The lateral surfaces of each bast-plate are therefore limited by one pluri- or multi-seriate medullary ray, which may be divided into one radial portion belonging to the bast-plate, which grows centripetally, and one belonging to the contiguous projection of wood, which grows in the main centrifugally. As a result of the non-uniform progression of its growth, a continuous displacement goes on between the two radial portions, in other words, between the lateral faces of the bast-plate and the adjoining ones of the woody projections; the two faces are not grown together one with another; in transverse sections, even of fresh internodes, a slit-like space often appears between the two; the bast-plate is in close tissue-connection with its surroundings only at the outer and inner sides. But, as has been already said, there is also a slow growth of wood from the portions of cambium at the base of the groove, and accordingly as this goes on, there succeeds a firm coalescence (and usually lignification) of the radial portions of the medullary ray, as far outwards as the formation of wood extends.

The finer structure of the wood shows no specially remarkable peculiarities in those species, which have been more exactly studied. Their bundles consist, e. g. in Bignonia (Anisostichus Bur.) capreolata[1], of wide-pitted vessels, narrow spirally thickened pitted vessels, and vessel-like tracheides, wood-fibres, paratracheal bundle-parenchyma, and intermediate fibres: they are traversed by numerous one- or few-layered medullary rays, to which may be added the four at the limiting faces of the four portions of wood which are superseded. These latter portions, besides their limited development, are distinguished from the rest of the wood in the species named by their denser structure, resulting from the absence or paucity of wide pitted

[1] Compare Sanio, Botan. Zeitg. 1863, p. 407.

vessels. This difference between the superseded and the projecting bands of wood is absent in other species. The genus Clytostoma is, according to Bureau, distinguished from most others by very dense compact wood, with very narrow vessels; also, the cortex is generally of normal structure. The bast consists of normal soft-bast, which is traversed by narrow concentric continuous zones of bast-fibres. In the bast-plates the first-formed secondary zones of soft bast are specially narrow, and but little thicker than the zones of fibres alternating with them; those which are formed later are often on the average of much larger, but alternately variable, radial diameter. The soft bast consists, especially in the plates, of sieve-tubes, mentioned in Chap. V, which are usually wide, and are surrounded in the usual way by delicate cambiform cells. Here also there are various special differences according to genera and species.

The phenomena hitherto described are uniform for all climbing Bignoniaceæ with four intruding plates of bast. Exceptionally, and as an individual peculiarity, the number five is found instead of four. As regards further conditions, there are variations which are in exact correlation with the generic differences founded on the formation of flowers and fruit.

The number of the superseded bands of wood and intruding bast-plates in a number of genera remains always limited to four as described. In numerous others, on the other hand, in addition to the four primary plates there appear successively new ones in addition as the growth in thickness proceeds: these from their origin onwards behave in all points like the similar primary ones, and in ordinary regular cases are so arranged that each bast-plate of next higher order divides the protrusion of wood, on which it appears, into two almost equal lobes (Fig. 226). All bast-plates of the same rank arise almost simultaneously, and therefore intrude an almost equal distance inwards, the lobes of the wood, successively increased from 4 to 8, 16, 32, therefore show a regular dichotomous division and arrangement. When the stem has grown very old, these conditions may become less regular.

In many genera each single bast-plate has exclusively the phenomena of growth above described, and therefore always remains equally broad throughout. In others, however, the plates become gradually broader outwards in the following manner: opposite each protruding mass of xylem, after it has grown in thickness to a certain extent, the radial band limiting the bast-plate itself hangs back in its growth, while the portion of cambium adjoining it forms a narrow bast-plate in the manner above described, and is joined laterally on to that first present. Since the same process is repeated periodically—perhaps with each annual layer—as the growth in thickness proceeds, each bast-plate becomes broader outwards, by step-like increments on both sides. Each step-like portion of it, as well as the superseded radial band of wood belonging to it, has the properties above described for the primary ones. According to the individual case, each successive order of steps arises at the two sides of one plate, and of all the plates of one transverse section of a stem at a more or less equal distance from the middle; the whole arrangement of steps is therefore to a variable extent regular or irregular. Comp. Figs. 225, 226.

The widening of the bast-plates outwards, as described, is continuous, if the segments of wood, which adjoin the successive steps, widen in their further increase in such a way that the limiting faces remain exactly radial (Fig. 225). But in

certain genera it happens that the segments of wood at the sides of the bast-plates grow during the increase in thickness, not only in a radial direction, but also tangentially, and become successively broader, so that they press against the bast-plate, and squeeze it together, displacing and destroying its elements. The same process is repeated in the successive steps, so that old plates are alternately broader, and reduced to quite narrow bands by step-like corners, which encroach simultaneously upon them, those from opposite sides often coming into contact, and even overlapping one another. Comp. Fig. 226.

In addition to these diversely varied phenomena there appear finally in the old stem in certain genera, sometimes concentrically renewed rings of growth, sometimes splittings of the first by subsequent intercalary growth; this will be discussed in later paragraphs.

The roots of the plants in question have, according to Crüger, in many species the same lobes, with intruding bast-plates as the stems, with this difference, that the number and arrangement of the lobes and plates are less regular. Bureau's statements contradict this, even in Bign. Unguis, which is specially quoted by Crüger, since according to the former bast-plates do not occur, but the thick masses of the xylem composed of vessels and wood fibres are only variously cleft by bands of parenchyma, which sometimes intrude radially, while sometimes they are arranged transversely, and connect the radial bands in a reticulate manner. In the tuberous swellings of the roots, which are characteristic of the genera Glaziovia Bur. and Bignonia Bur., the parenchyma is largely developed between relatively small vascular and fibrous strands. In these cases therefore there is simply the structure of parenchymatous roots. Also in branch-roots two to three years old of An. capreolata I do not find the characteristic stem structure. The xylem is in transverse section only slightly undulated, composed of sclerotic elements, with medullary rays of one or a few rows of cells; the bast-layer is thin, with few relatively small sieve-tubes, and small scattered groups of fibres at the outer limit; the cortex, as noted on p. 547, is persistent, and composed of thin-walled parenchyma surrounded by a superficial periderm.

The generic anatomical characters of the stems of the Bignoniaceæ, founded by Bureau, are based partly on the combination of the different phenomena above described, partly on special conditions of structure of wood, cortex, and periderm; and, finally, on the general form of the stem. Since it is of interest to have a complete knowledge of the differences of structure and growth, which obtain within a narrowly circumscribed group of nearly allied plants, corresponding in their mode of life and adaptation, and which are in correlation with the generic characters taken from the reproductive organs, we may here briefly reproduce Bureau's synopsis[1], awaiting further explanation of the cases marked *.

I. Stem always with only four intruding bast-plates.

A. Bast-plates always equally broad throughout. (Comp. Fig. 224.)

(*a*) Without subsequent renewed formation of wood in the cortex.

1. Surface of the cortex with a thin periderm: *Arrabidæa* DC.

2. Surface of the cortex with a thick layer of cork when old: *Paragonia*, Bur.

(**b*) With subsequent renewed unilateral formation of wood in the cortex and irregular form of the stem resulting from it: *Callichlamys*, Miq.

B. Bast-plates widened in a step-like manner outwards. (Comp. Fig. 225.)

a. Stem cylindrical or ridged without channels on the ridges.

(*a*) Without stony elements in the cortex.

a. Steps of the bast-plates broad, i.e. of the width of several segments of wood separated by small medullary rays.

[1] Compare Bull. Soc. Bot. de France, *l. c.*

1. Stem cylindrical or hardly four-cornered, bast-plates remaining a long time of the same breadth, then with high irregular steps: *Petastoma* Miers.
2. Stem cylindrical, with fine longitudinal furrows, subsequently thrown off. Steps of the bast-plates appearing late, broad, and few in number: *Stizophyllum* Miers.
3. Stem cylindrical with four narrow furrows. Bast-plates broad. Steps present from an early age, as broad or broader than high: *Cuspidaria* DC.
4. Stem, at least when old, four-cornered; cortex uneven, with many lenticels. Bast-plates with regular steps, and one broad medullary ray between each two step-like bands: *Tynanthus* Miers.

β. Steps not broader than the space between two medullary rays of the wood. Stem cylindrical. Bast-plates with a very broad middle lamella: *Fridericia* Mart.

(*b*) Stony sclerenchyma in the cortex.

1. Stem somewhat flattened opposite the bast-plates. Bast-plates short, somewhat widened. Steps not broader than the space between two medullary rays of the wood. Stony elements only distributed in the outer cortex, and in small quantity in the primary bast: *Tanæcium* Sw.
2. Stem cylindrical. Steps of the bast-plates few. A continuous ring of stony elements 6–7 layers thick beneath the surface: *Adenocalymma* Mart.

b. Stem when young with four projecting ridges, these are later thrown off, and replaced by channels (comp. Fig. 225). Steps of the bast-plates broad, irregular: *Pleonotoma* Miers.

C. Bast-plates partially constricted and destroyed by pressure through tangential widening of the zones of wood. Young branches octagonal. Angles thrown off later. The old stem cylindrical. Cortex thick: *Pithecoctenium* Mart.

II. Bast-zones successively 4, 8, 16, 32.

A. Wood always without displacement or separation of the older zones through subsequent intercalary formations.

a. Without subsequent formation of wood in the cortex.

(*a*) Young shoots cylindrical, without ridges which may be thrown off.

α. Stony elements in the outer cortex, and very numerous in the outer region of bast. Bast-plates with very irregular steps: *Phryganocydia* Mart.

β. Without stony elements in the cortex.

† The four first bast-plates long and narrow, the rest short and broad. Cortex with red colouring matter: *Cydista* Miers.

†† All bast-plates of similar form. Cortex without the red colouring.

1. Stem twisted like a rope, with eight external rounded projections. Bast-plates of successive age differing little in length, all very narrow and with few steps; the four first with broad closely arranged medullary rays externally. Cortex without sieve-tubes[1]: *Pyrostegia* Pr.
2. Stem not rope-like. Wood very dense, with very narrow fibres and vessels. Bast-plates very numerous, steps high, broad, irregular, medullary rays between the middle and the lateral lamellæ of a plate hardly any broader than the rest. Pith very narrow: *Clytostoma* Miers.
3. Stem not rope-like, or only slightly so. Texture of the wood loose and porous. Steps of the bast-plates very few. Medullary rays between

[1] 'Pas de cellules grillagées dans l'écorce' (? Author).

the middle and the lateral lamellæ broad and obvious. Pith broad, breaking down in the middle: *Anemopægma* Mart.

4. Stem not rope-like. Numerous bast-plates with very narrow steps and a broad medullary ray on each side of their middle lamella: *Lundia* DC.

5. Stem rope-like. Wood with wide vessels. Bast-plates variably constricted, and destroyed by pressure by the adjoining steps of wood (sometimes formation of wood in the cortex, opposite the bast-plates*): *Distictis* Mart.

(*b*) Young shoots with six ridges thrown off later: old ones cylindrical, cortex thin. Numerous very unequal bast-plates with irregular steps: *Amphilophium* Kth.

(b)* Stem with concentric (renewed) rings of wood in the cortex.

1. Stem not rope-like or slightly so. Medullary rays of almost equal breadth: *Haplolophium* Cham.

2. Stem rope-like. Medullary rays of very unequal width: *Glaziovia* Bur.

B. * Inner layers of wood split up in the old stem by subsequent intercalary formations of parenchyma, wood, and bast.

(*a*) Wood with annual rings. Segments of splitting few. In the bast-layer are wood bundles, at first fan-shaped in transverse section, but soon rounded off: *Anisostichus* Bur. (Figs. 224 and 237.)

(*b*) No annual rings. Segments of splitting numerous, repeatedly cleft, between them newly formed parenchyma. The segments at the middle of the stem turned in all directions.

1. Segments of wood at the middle of the stem three-cornered, undivided, all others dichotomously split: *Melloa* Bur. (Fig. 226.)

2. All wood-segments, both those in the middle and those at the periphery of the stem, dichotomously split: *Bignonia* Bur.

Sect. 184. The structure and growth of the internodes of species of *Phylocrene*[1] correspond in their main features with those of the climbing Bignonias. The differences between the two consist partly in differences of the more minute structure of wood and cortex, partly in this, that the number of the original protrusions of wood and intruding plates of bast is not four, but usually eight in the specimens examined, more rarely thirteen, numbers which appear to vary with the individual. Subsequent divisions of the original protrusions of wood by secondary plates of bast have not been observed, but on the other hand there are sometimes pauses in the activity of the first cambium, and zones of renewed growth then appear in the cortex. Comp. Sect. 191.

As regards the relations of structure the following facts may be brought forward, reference being made to the description of Mettenius, and Mohl's supplement to it. (Fig. 227).

The pith is surrounded by a narrow uniformly thick, ring-like zone of wood (medullary sheath), which includes between the slightly thickened cells the primary vessels arranged in radial rows, usually in pairs opposite the protrusions of wood. This zone passes over externally into one which is also annular, and is composed of numerous successively wider pitted vessels, thick-walled fibrous elements, fascicular parenchyma, and narrow medullary rays. This zone of pitted vessels, retaining fundamentally the

[1] Griffith, in Wallich, plant. Asiat. rarior. III. p. 216, after Lindley, Introduction to Botany, p. 69.—A. de Jussieu, *l. c.*—Tréviranus, in Botan. Zeitg. 1847, p. 400.—Mettenius, Beitr. z. Botan. p. 50.—v. Mohl, Botan. Zeitg. 1855, p. 878.

same structure, is continuous externally into the equidistant protrusions *h*, which are wedge-shaped in transverse section. With the exception of their inner portion which belongs to the medullary sheath, the intervening bands of wood, which hang back in their growth in thickness, consist, on the other hand, for the most part of thin-walled cells arranged in radial rows, amongst which are scattered isolated pitted vessels, each being accompanied by a few thick-walled elements. The bast plates (*b*) consist in the main of the large, sharply ended sieve-tubes mentioned in chap. V; these lie very regularly in radial or tangential rows, being usually separated from one another in a radial direction by single, triple, or quadruple concentric series of narrow elements (Fig. 228), rarely they are arranged contiguously in pairs; in a tangential direction, however, they are usually in immediate connection, being rarely separated by the narrow elements (Fig. 228). These narrow elements are for the most part sclerenchymatous fibres, less frequently delicate cambiform cells, of which usually 1–2 abut on each sieve-tube, as seen in transverse section. The peculiar distribution of the thick-walled and other elements causes

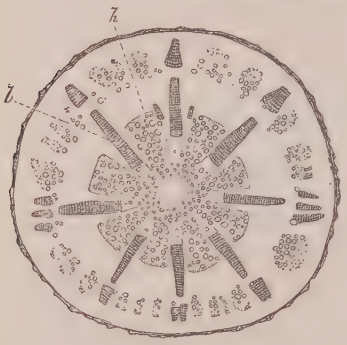

Fig. 227.

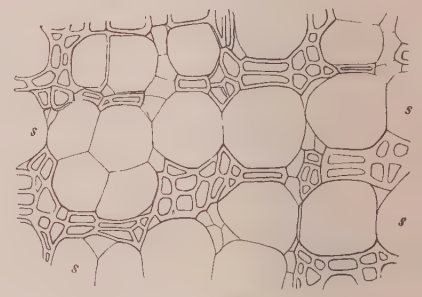

Fig. 228.

FIG. 227.—Phytocrene spec. Transverse section of the stem, × 2, from the same material as that described by Mettenius; *h* the eight protrusions of the porous wood; *b* the bast-plates between them. Laterally from one of them, and to the right of the wood-protrusion marked *h*, are two small similar ones. Parenchyma of pith and cortex are left white. Externally to the inner circle of growth is one of renewed growth, which shows several bundles, between broad parenchymatous medullary rays, opposite each of the inner protrusions of wood; these consist of a relatively large xylem, constructed similarly to the latter, and an extremely small bast portion; and opposite each of the inner bast-plates is one bundle, or at most two to three, constructed like the latter, which have only a very small xylem at their inner side. The latter could hardly be indicated in the Fig.

FIG. 228.—Portion of a bast-plate from Fig 227 (× about 140); *s*—*s* sieve-tubes. The narrow meshes of simple contour abutting on these are transverse sections of the cambiform cells; the elements with a strong double contour are bast fibres.

the almost chess-board-like appearance of the plates; at the outermost oldest parts of them the arrangement is less regular, the sclerotic elements are in larger proportion. A multiseriate broad medullary ray, consisting of very delicate cells, limits each lateral face of the bast-plate, and is continuous towards the pith along-side of the superseded band of wood. It appears, as in the Bignonias, to consist in not very young specimens of two radial portions, which undergo displacement. There are at least indications of a step-like external widening of the bast-plates. Externally from the zone of cambium surrounding the protrusions of wood, that is in the normally arranged layer of bast, there are scattered irregularly, here and there, small irregular groups of the same sort of tissue as that which composes the bast-plates. With the exception of these groups it appears from transverse sections that the bast layer in question contains no sieve-tubes in by far its greater part, but is composed rather of thin-walled parenchyma only, with isolated thin sclerenchymatous fibres.

The above description is derived partly from Mettenius' account, partly from the same transverse sections of the stem as the latter was based upon. Some other transverse sections, and the figure in Lindley *l. c.*, show a structure which differs in many details from that described. But whether we have to deal with individual or specific differences is uncertain, since there were no definitions of the species in the material used. According to Jussieu[1] there is also in Phytocrene a formation of dichotomous lobes of the protrusions of the wood.

Sect. 185. Similar phenomena to those in Bignonias and Phytocrene, with similar differences to those between these plants, are found developed to a different extent in the climbing shrubs of different other families: within the cylindrical or slightly ridged stem are flat, or very deep infoldings of the xylem, and bast-plates of corresponding form, which fit into these. Disregarding certain of the cases in question which are not defined with certainty, and are not very typical, we may here name members of the Malpighiaceæ, from the genera Tetrapterys, Banisteria, also Stigmaphyllon[2], and Peixotoa sp.[3], Apocyneæ of the genera Condylocarpon[4], Echites; the Asclepiad Gymnema silvestre, a species of Celastrus[5], and a Tournefortia[6].

The *Peixotoa* (*l. c.* Fig. 2) shows eight blunt low protrusions of the xylem, within the cylindrical outer cortex, which is surrounded by great rent masses of cork or bark. Müller's *Tetrapterys* (*l. c.* Fig. 1) shows very similar phenomena to those in the Bignonias above noticed, p. 574 under II. In the younger round stems or branches, up to 1^{cm} in thickness, the xylem has six sharp incisions, filled by bast-plates; in stronger stems there appears in addition to these, and accompanying their radial development, a further single or double splitting of the protrusions of xylem by intruding bast-plates, that is a formation of dichotomous lobes of the transverse sections of the xylem. The older parts of the bast-plates are constricted and pressed together by tangential extension of the adjoining portions of xylem. It is uncertain whether the radial lateral faces of the bast-plates remain surrounded by a layer of cambium.

In Müller's *Condylocarpon* (*l. c.* Fig. 4) the transverse section of the xylem of young branches up to 1^{cm} in thickness is round, and equally thick on all sides. Then begins the formation of incisions and of bast-plates fitting them—the number of those which appear at first and simultaneously seems to be three; in addition to the first, which grow further in a radial direction, numerous fresh ones of similar character successively arise, so that the whole system shows numerous irregular dichotomous lobes as seen in transverse section. Here also there is found in older inner parts, for certain distances, contraction and complete distortion of the bast-plates by swollen protrusions, which subsequently appear at the lateral faces of the protrusions of xylem; here also it remains to be investigated whether they arise from a cambial zone which is permanent from the first at this point, or from one which appears subsequently.

Sect. 186. An anomaly in the distribution of tissues, which goes a step further than those hitherto spoken of, consists in the following peculiarity of certain woody plants, viz. that they develope rings of wood, cambium, and bast in their normal position, and without specially remarkable relations of form, but develope no *sieve-tubes* in the secondary bast, these being united with delicate parenchyma in bundles, and *enclosed in the xylem.*

[1] *l. c.* p. 122.
[2] A. de Jussieu, *l. c.* p. 106.
[3] Fr. Müller, *l. c.*
[4] Idem, *l. c.*
[5] Jussieu, *l. c.* p. 117.
[6] Crüger, Botan. Zeitung. 1851, p. 468.

This phenomenon occurs in *Strychnos*, in all investigated species of the genus, both in those which climb and grow with tendrils—S. colubrina, toxifera, multiflora, and that not exactly defined form figured by F. Müller[1]—and also in the tree- and shrub-like species—S. nux vomica, brachiata, and innocua. It appears further, though in a different form to that in Strychnos, in that member of the Malpighiaceæ mentioned by F. Müller[2] as *Dicella* spec.

The above-named species of the genus Strychnos were investigated in dry material; for the investigation of the youngest stages of development a living specimen was used of the plant, which comes to the shops as S. nux vomica, a plant which really belongs to another species.

The species of Strychnos have a normally arranged ring of bicollateral bundles of the trace in the young internode. Their externally directed (external) phloem, in which, on the first differentiation of the bundles, the first developed elements (Protophloem) may be recognised, consists in the fully elongated internode of small groups of about 4–6 narrow elements, which are very similar in transverse section to small groups of sieve-tubes. But I will not say definitely whether they really contain developed sieve-tubes. After those primitive phloem-elements the first vessels appear at the inner margin of the xylem, and almost simultaneously with them the phloem-groups of the inner margin begin to become plain. The further development of the xylem then proceeds in the manner normal for Dicotyledons: in the inner phloem-groups the increase and growth of the elements continues for a long time, and they attain a great size. Numerous intermediate bundles, separated from one another by medullary rays one layer of cells thick, then connect the bundles of the trace into a dense ring. The intermediate bundles contain also, at least in part, the small external phloem-groups, but no internal ones: at least they are certainly absent in most cases. An increase of the elements of the small external phloem, in the same way as in the typical Dicotyledons it keeps pace with the growth of the xylem, does not occur in Strychnos; but rather that layer of cells immediately adjoining those small external phloem-groups, or at least the next inner one, passing round the stem, becomes the mother-layer of the cambium. The origin of this, as could be proved with the small quantity of material available, is fundamentally the same as in normal Dicotyledons; the same is the case with the direction of the divisions which produce the secondary elements. In the succession of these, however, and in the development of their products, the peculiarity occurs that they at first proceed almost exclusively in a centrifugal direction: it is exclusively or almost exclusively secondary wood that is developed. In a one-year-old shoot, 1^{mm} thick, of the living plant, the xylem-ring of which showed on the radius of a transverse section 10–12 elements, and among them wide vessels, there lay in each radial row, between the outermost mature xylem elements and the small external phloem-groups, only two cells, separated by one tangential wall, or even only one thin-walled cell. These belong to the cambium and zone of increase, the latter is thus directly contiguous with the primary zone of bast: it forms with this a narrow ring round the xylem, limited externally by a dense layer of short sclerenchyma. This condition remains for a long time; in a dry branch of S. nux vomica $2{\cdot}5^{mm}$ thick I find the bast layer not at all or but little

[1] *l.c.* Fig. 10.

[2] *l.c.* p. 59.

thicker. But later a change takes place: a dry piece of a stem or branch of S. nux vomica of 135mm diameter, which was investigated, had a bast zone about 5mm thick, consisting of very many layers. Climbing species, such as S. toxifera, S. brachiata, &c., seem to form secondary bast in still larger quantities. The secondary layer of bast has, except in one essential point, the same structure, and shows the same phenomena of dilatation as in the Dicotyledons with normal growth. Especially in S. nux vomica, it consists of broad, uniformly delicate, parenchymatous medullary rays, without stony elements, and between these run narrow bands, corresponding to the strands of xylem, each consisting of a few longitudinal rows of elongated cells with oblique or horizontal ends, soft, rather thick, lateral walls, with simple scattered pits, and delicate transverse walls. The strands are accompanied by numerous chambered sacs with crystals. Both bast fibres and sieve-tubes are entirely absent. *The sieve-tubes are on the other hand situated in the wood.* This has in the main the normal structure of Dicotyledonous wood. It consists in the species in question of (1) broad, numerous, medullary rays, composed of procumbent cells; (2) narrow strands, and portions of strands of different grades, which are composed of irregularly alternating broad transverse zones of very thick and long wood-fibres on the one hand, and large-celled fascicular parenchyma with pitted vessels on the other. In the mass of wood, which by reason of this composition appears, in a slightly magnified transverse section, to be marked with irregular bands, there lie numerous strands, on an average about 0·30mm thick, with a roundish, or broadly elliptical transverse section. They are scattered through the whole annual ring, being usually isolated between two medullary rays, and rather broader than the section of wood which bears them, so that they intrude on both sides into the adjoining medullary rays; sometimes they also pass transversely through 2–3 strands of wood, together with the intervening medullary rays. Their longitudinal course follows in the main that of the xylem-strands, with this difference, that they show fewer acute anastomoses than these. These strands are composed of longitudinal rows of thin-walled colourless cells—and their circumference seems to be covered exclusively by these,—and numerous large sieve-tubes, with oblique endings of the joints, bearing sieve-plates arranged in a ladder-like manner. Suitable stages of development show easily that these phloem-strands in the xylem are derived internally from the cambium (comp. Fig. 229). Other species investigated show similar, sometimes even larger phloem-strands in the xylem, and, as far as may be decided from dry material, the same absence of sieve-tubes in the bast. All investigated species have, at the limit

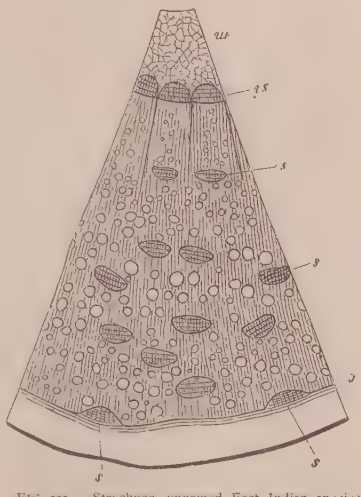

FIG. 229. — Strychnos, unnamed East Indian species. Portion of a transverse section through a branch (20); *m* pith, *c* cambial zone, between the two is the xylem with numerous large vessels, *ss* bundles of sieve-tubes at the limit of the path; *s* the same in the xylem, the two outermost at the limit of the cambial-zone, just passing off from it.

between bast and outer cortex, a massive persistent ring of strong sclerenchyma, and usually single sclerenchymatous fibres at the outer side of it. In S. brachiata and toxifera there are besides large groups of strong sclerenchyma in the secondary bast. The parenchymatous outer cortex forms in all of them a thick periderm at the outer surface, and especially in S. innocua, a thick soft mass of cork. On the structure of the wood of other species it need only be remarked, that it is distinguished from that of S. nux vomica by the relatively much larger quantity of thick fibres, otherwise it shows no generally remarkable properties. The details still require more exact investigation. In allied Loganiaceæ, I found in Logania longifolia and floribunda bicollateral bundles of the leaf-trace, but normal bast, and no sieve-tubes in the xylem. Gaertnera longifolia, Sykesia spec., and Fagræa lanceolata show a perfectly normal Dicotyledonous structure, and no bicollateral bundles of the trace.

Of the *Dicella* above-named only a few dry pieces of the stem about 5–6^{mm} thick, sent by Fr. Müller, were available; some of these were round, some very eccentrically developed. The round pith is immediately surrounded by a uniform ring, about eight cells thick, of narrow ordinary xylem elements, arranged regularly in radial rows. The other secondary wood consists chiefly of thick-walled pitted vessels and fibres, with uniseriate medullary rays, partly also of masses of thin-walled tissue composed of wide parenchymatous cells, sieve-tubes, and narrow sacs with conglomerated crystals, which are marked off from the thick-walled mass by an almost unbroken layer of partitioned crystal-sacs with small klinorrhombic crystals. This delicate tissue, with sieve-tubes, is distributed in the thick-walled vascular tissue in the form of anastomosing flat strands, which appear in transverse section as irregular concentric segments of a ring, of very unequal size and form, often with sinuous curvature, and frequent anastomoses. These form bands and zones in the transverse section, which are embedded in the hard mass of xylem, and are, on the average, smaller and narrower than the hard portions, which alternate with them; these phenomena give the whole transverse section a peculiar, finely banded, almost marbled appearance. As far as could be made out from the dry brittle material, the whole mass of wood described arises on the inner side of a delicate one-layered zone of cambium. This is surrounded by a thin cortex, which shows no peculiarities worthy of mention, beyond the fact that in the secondary zone of bast, which contains narrow scattered fibres, and many small conglomerated crystals, sieve-tubes were not to be found.

Further details of structure have been in part purposely left unnoticed in the above notes, both in Strychnos and Dicella, in part they require still further investigation.

Sect. 187. The appearance of a ring of *cambium* and secondary thickening on the *inner side* of the external, normally growing ring of wood, has been discovered by Sanio [1] in the stem of Tecoma radicans. The bundles of the leaf-trace of the normal bundle-ring [2], with the exception of those perpendicularly below the next higher pair of leaves, are bounded, when young, on the side next the pith, and opposite the primordial spiral vessels, by a small strand of delicate cells, which remain narrower than those surrounding them. The innermost group of cells of each bundle, which abut on

[1] Botan. Zeitung. 1864, pp. 61, 228.

[2] Compare Nägeli, Beitr. I. p. 107.

the large-celled pith, and are formed by longitudinal divisions facing in all directions, soon ceases to grow (single rows of them may develope into sieve-tubes). The outer layers develope into elongated, afterwards thick-walled parenchyma. When the normal cambium has begun its growth at the outer side of the ring of wood, radial extension and tangential division begins in a middle layer, and this process is extended, as in the origin of a normal cambium, from each group laterally over an annular layer running along the whole inner side of the ring of wood. This now forms, as in a normal cambium but in a reversed direction, wood and bast, the former being affixed to the zone of parenchyma which covers the inner surface of the ring, and pushing the bast towards the pith. Both products of the inner cambium resemble in their structure the secondary wood and bast of the normal outer ring, and have, like them, both medullary rays and annual rings. Their naturally very limited growth compresses the originally broad pith more and more. It remains to be investigated how long the process lasts, when it is terminated mechanically, perhaps after the complete compression of the pith, and what relation it has to the frequent splitting of old stems.

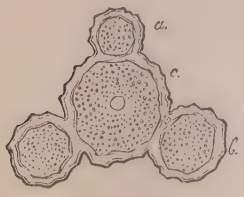

FIG. 230.

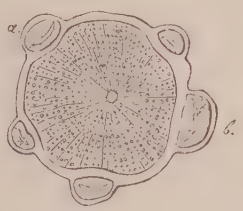

FIG. 231.

FIG. 232.

FIGS. 230, 231.—Transverse sections through stems of not exactly defined species of Serjania or Paullinia. Natural size. From Schleiden, Grundz. *a b* outer rings; *c* the main ring of the compound woody body. The cortex is white in both figures, the xylem (in the strict sense) dotted according to the distribution of the vessels. Medullary rays obvious in Fig. 231, in 230 not obvious; also the pith is not shown in the outer rings of the latter figure.

FIG. 232.—Serjania caracasana. Transverse section through a young internode just above the node (10). After Nägeli. Within the ring of sclerenchyma *s* are the main ring *h* and four outer rings; to the left below is one outer ring opening into the main ring. The dark prominences of the rings pointing towards the pith are the primary bundles of the leaf-trace.

Indications of a similar formation appear, according to Sanio[1], to occur in Rumex crispus, but further investigations are necessary on this point.

SECT. 188. **Several partial cambiums and rings of growth, lying side by side** in the same transverse section, appear in the most exquisite development in the woody stems, so often described since Gaudichaud[2], of climbing Sapindaceæ of the genera *Serjania*, *Paullinia*, and *Thinouia*. The transverse section of the stems in question shows several separate rings of wood surrounded by a common cortex, and in most of them a larger main ring occupying the middle, and several smaller outer rings arranged in a circle round it (Figs. 230, 231); more rarely five, or in exceptional

[1] Botan. Zeitung. 1865, p. 179.

[2] Récherches, &c. *l. c.* Tab. XVIII.—Compare further A. de Jussieu, Monogr. des Malpighiacées, *l. c.*—Schleiden, Grundzüge (3 Aufl.) II, p. 166.—Tréviranus, Botan. Zeitung. 1847, p. 393.—Crüger, Botan. Zeitung. 1851, p. 481.—Schacht, Lehrbuch, II, p. 58.—Netto, Comptes rendus, tom. 57 (1863), p. 554, and Ann. sci. nat. 4 Sér. tom. 20, p. 166.—Nägeli, Dickenwachsthum d. Sapindac., compare p. 463.—Radlkofer, Atti del Congresso Botan. ten. in Firenze, 1874, p. 60, and Monographie d. Gattung Serjania, München, 1875. [Also, Radlkofer, Entstehung d. secundären Holzkörper im Stamme gew. Sapindaceen Naturforscher, Vers. z. München, 1877.]

cases 6–7, peripheral rings without the central main ring. Radlkofer calls the first-named structure a *compound* xylem, the second a *divided* xylem. In both cases each woody ring is surrounded by a normal, permanently active zone of cambium, and also by a normal layer of bast. Each encloses a pith, which is often inconspicuous, immediately around which Jussieu showed that there were spiral vessels. Following them in a longitudinal direction, it is found that the wood- and bast-rings run side by side in the internodes; at the nodes they are connected one with another, in a manner to be described below, so that as regards the compound xylem the opinion might arise that the small outer ones might be the wood and bast of axillary branches joined longitudinally to the main stem. The composition described is found in the stems from the commencement of differentiation of tissues onwards. (Fig. 232.)

We are indebted to Nägeli's investigations of the development of a number of forms with compound xylem for a proper understanding of this structure.

The main results of these are summarised below, partly in the author's own words: we must forego even a short statement of the individual phenomena in one species, and the differences in different species, because of their complication, reference being made to the original work.

The stalks or stems of the plants in question are ridged from the very first; the leaves are spirally arranged; from the axil of the leaves arise a branch and a tendril as axillary shoots. The course and development of the primary bundles correspond to the main rules which hold generally for Dicotyledons (Chap. VIII). At each node three bundles of the trace, and two axillary bundles of the trace, enter the stem. They show generally a tangentially-oblique course, which deviates more or less from that of the angles of the stem. The median bundles have a tendency to unite into three sympodia. Both sorts of bundles of the trace have usually a radially-oblique course; from their point of entry into the node to their insertion on a bundle of a lower node they pass further and further from the surface of the stem. All bundles are collateral, often perhaps[1] bi-collateral.

In many forms, which correspond closely to those here to be discussed, such as the Cardiospermum, described by Nägeli, Paullinia sp., and Serjania Mexicana, the bundles of the trace appear in the transverse section of the young internode at very different distances from the middle; they surround a prismatic pith, which has projecting angles, and even infolded sides. Nevertheless, they are connected by a normally arranged, general layer of cambium, and together form a simple wood and bast body of the Dicotyledonous type, which is normal and remains so, though of angular and infolded outline.

In other forms, however, with a strongly oblique course of the bundles, the infoldings of the primary ring of bundles become so deep that single groups of bundles are as it were nipped off, to continue the metaphor, externally from the ring, and excluded. The bundles of such a group are at various distances from one another, and from the middle of the internode. The bundles of the group, which are external as regards the latter, have their xylem and phloem placed normally

[1] Compare Nägeli, *l. c.* p. 35.

relatively to it, i. e. the former is turned towards the middle of the stem. In the others this orientation is so inverted, that all the xylem-portions of one excluded group face towards one common middle point situated within the group itself. A bundle may belong successively, in its obliquely longitudinal course, to different sides of one excluded group, and to the main ring, and must therefore undergo successive rotations.

These arrangements appear on the first differentiation of tissues; they even hold for initial bundles still surrounded by meristem. As the differentiation of tissues proceeds, the main ring, together with the pith surrounded by it, assumes the above-indicated normal properties. Each excluded group does the same; the strand of meristem lying between its opposite xylem-masses developes into parenchymatous pith; at the limit of its xylem and phloem a normal cambium appears all round. The corresponding narrow bands of meristem between the main ring and the outer rings assume the structure of (chiefly parenchymatous) cortical tissue, which is continuous into the general outer cortex. As may be concluded from what has been said above, the arrangement and form of the rings within this general sheath vary in successive transverse sections; in general, according to the rule formulated by Nägeli, an external ring, followed upwards and downwards, remains intact and unaltered as far as the next node. Here it opens into the main ring, whereby the primary bundles alter their mutual positions, and are continued on the other side of the node as an outer ring or as a fold. (Comp. Fig. 232.)

The histological composition of the mature parts shows, as far as the not very thorough investigations extend, no fundamental differences from the normal structure of wood and cortex. The presence of a many-layered ring of sclerenchyma at the inner limit of the surrounding outer cortex (Fig. 232) is general. This is at first completely closed, and is burst by the progressive dilatation, and split with the same phenomena, as were noticed on p. 543 for Aristolochia Sipho.

In the genus Thinouia in perennial stems there appear, in addition to the phenomena described, cortical zones of renewed growth, as in the Menispermeæ and Leguminosæ. According to Crüger's drawings[1], which may here be quoted, these appear very irregularly arranged, sometimes as portions of concentric rings, sometimes as isolated bundles. If I understand Netto rightly, subsequently renewed peripheral zones appear even in species with an originally simple ring of xylem.

Radlkofer's *divided xylems*, which are peculiar to a definite group of the genus Serjania, are distinguished from the described compound ones, as above indicated, solely by this, that only five, rarely six to seven, peripheral partial rings are formed, without the middle or main ring. Five (or six to seven) groups of bundles bulging strongly outwards, which only anastomose at the nodes, are present from the first; each grows by means of a surrounding cambium into a ring, which is in itself normal.

According to Radlkofer's investigations most of the numerous genera of the Sapindaceæ contain only species which do not climb, and show a normal stem structure. Twining and climbing species occur in the genera: *Cardiospermum* with non-woody stem, and angular but normal xylem; and *Serjania*, *Paullinia*, *Urvillea*, and *Thinouia* with

[1] Botan. Zeitung. 1851, Taf. VIII.

perennial woody stems. But not all the species of these genera are Lianes, nor have all which are so an anomalous structure; many have only an angular or lobed, but otherwise normal xylem.

Of the 145 species of the genus Serjania 84 have the above-described compound xylem, five have divided xylem. The structure of the xylem, and especially the modifications of the compound xylem, in number, relative size, special form and structure of the outer rings, are always correlated with the other characters, according to which the subsidiary groups of the genus are separated. The five species with divided xylems also form a natural group according to other characters.

Of the still more numerous species of Paullinia twelve have an anomalous and compound xylem.

Thinouia is characterised by the above-described subsequent appearance of cortical zones of wood at the periphery of the compound wood; whether this applies to all the 8–10 species of the genus is not certain.

Of the species of the genus Urvillea, which are also 8–10 in number, anomalous structure is known only in U. lævis, and here it differs fundamentally from that of the other Sapindaceæ, and will be noticed in Sect. 193.

Sect. 189. In the stem of the *Calycantheæ*, as described on p. 257, the leaf-trace bundles form the bundle-ring, while four of those bundles traverse the cortex. The former developes into a normal wood and bast with normal cambium; the cortical bundles grow by partial cambiums into those cortical bundles discovered by Mirbel, and since his time so frequently described[1]; these grow in thickness as long as the stem lives. The cortical bundle is collateral, and is composed at first of a small xylem and a stronger phloem, extended transversely; its orientation is inverted, i. e. the phloem is turned inwards, towards the ring of wood, and the xylem outwards. The latter directly abuts externally upon the broad, almost even, inner face of a strong bundle of sclerenchymatous fibres, which is almost half-moon shaped in transverse section: it is so surrounded by the phloem that the lateral margins of the latter also are in contact with the fibrous bundle. The limiting layer between xylem and phloem remains active as cambium, forming wood on the side next the former, and on the side of the phloem a zone of bast, which embraces the wood. The cortical bundle grows in this way like a single normal strand of wood surrounded by its corresponding strand of bast, but retains the inverted orientation. Further, it retains approximately, in its transverse section, the form of a broad and blunt triangle, which it has from the first, if the fibrous bundle be included, and leaving out of account irrelevant changes and irregularities, which appear as the volume increases. In the first, and onwards to about the fifth year, the xylem of the bundle is extremely small compared with the phloem, consisting of only few elements, while the section of the latter already shows radial rows of many elements. Later it increases greatly in strength; it assumes the structure of a normal secondary strand of wood, divided by small medullary rays, and even shows annual rings. The bast-zone surrounding it only consists of elements of soft bast, and in the main at least of parenchymatous elements: sieve-tubes remain still to be sought for. Its older layers suffer changes of dilatation as in the normal bast, according as they pass away from the zone of cambium; by their own growth, and by the pressure caused by the layer of periderm

[1] Compare p. 257. A complete list of the literature is given by Woronin, *l. c.*

surrounding the cortex, they are squeezed into the very lacunar outer cortex of the stem. The external much dilated bast portion, which is sharply marked off from the less dilated younger bast, is Woronin's outer cambial zone. The general cortex, which surrounds the bundle, follows by dilatation the growth of the latter, and of the main ring of wood. In comparison with the latter, the growth in thickness of the cortical bundles is slight: in the stem twenty-three years old investigated by Woronin, the whole transverse section of the strongest scarcely reached 2^{mm}, while the main ring of wood was $45–55^{mm}$ thick. On the outer surface of the stem the cortical bundles form blunt weak prominences. In the very old stem investigated by Mirbel, which was $3^{ins.}$, that is about 80^{mm} thick, the four cortical bundles were as thick as the little finger.

An indication of cambiogenetic growth in thickness is found also in the concentric cortical bundles of many *Melastomaceæ* (comp. p. 339), since a zone of cambium surrounding the xylem increases the number of the elements in a radial direction. Considerable increase does not take place, at least not in investigated species, since the bundles are thrown off at an early stage, together with the outer cortex, as bark.

Sect. 190. **Partial cambiums with inverted orientation of their products of increase** are known to us through the writings of Schmitz[1] in the case of the rhizome of species of *Rheum*.

In the tuberous branches of the rhizome of R. officinale the collateral leaf-trace bundles form a normal bundle-ring, further increased by a normal cambium: it encloses a large pith, which increases in relative circumference with the strength of the branch. Through the pith when young there run transverse bundles, in closely superposed transverse zones, corresponding to the nodes: these bundles connect the bundles of the leaf-trace one with another, and with those of other traces in a reticulate manner, partly by transverse branches, partly by vertical ones, which run especially in the neighbourhood of the woody ring. Each of these connecting bundles is originally a bundle of elongated cambiform cells and sieve-tubes; they are continuous with the phloems of the bundles of the leaf-trace at the point where these curve out into the leaf. At a very early stage a cambial layer appears round each such strand of phloem, and forms on the one side strands of wood with much parenchyma, on the other side strands of phloem corresponding to these, both strands being split up by medullary rays. Further, the formation of bast is next the original strand of phloem, the bast-layer is in fact on the inner side of the cambium, but the xylem on the outer side. This extensive and continued growth produces a bundle, which grows to a thickness of more than 1^{cm}, and always retains the characteristic inverted arrangement of wood and bast. The numerous medullary rays with the same colouring matter as in the root (pp. 518, 524) give to the transverse section a marked radial striation. Sections of this sort constitute the 'streaking' and radiate circles[2] characteristic of the pieces of rhizome of the officinal Rhubarbs. The growth in thickness of the streaky bundles continues even after the growth of the pith has ended: the result of this is a partial compression of the pith and dis-

[1] Sitzungsber. der naturf. Gesellschaft zu Halle, Dec. 1874. Botan. Zeitung. 1875, p. 260.

[2] Compare Wigand, Pharmacognosie.—Berg, Atlas, Taf. XII.

placement of the bundles. The growth in thickness of the bundles further extends to their point of insertion on the bundle of the trace as it passes out into the leaf, and continues at the latter point even though the growing woody ring may have enclosed both portions. The streaky bundles therefore lie both in the pith and in the parenchymatous wood; they run, as the result of their original arrangement and subsequent displacement, in very different directions, their stellate transverse sections are therefore found both in sections cut transversely, and in other directions through the rhizome. The quantity of the streaky bundles is on the average the greater, the thicker the rhizome. Schmitz found the same phenomena in the rhizome of Rheum Emodi, but not in that of other species cultivated in this country (Germany).

Sect. 191. **Successively renewed thickening rings**[1] are a rather wide-spread phenomenon, which appears in very various special forms. The general course of the type of growth thus indicated is as follows. Both in the stem and root the secondary thickening begins in all respects normally, and often proceeds for a long time thus normally. Then there appears in the parenchyma, outside the normal first cambium, a secondary meristem, formed chiefly by tangential divisions; it usually starts from single points, and then extends laterally: in it corresponding strands of wood and bast separated by medullary rays are differentiated. These are themselves arranged like a normal Dicotyledonous ring of secondary thickening: wood and bast are permanently separated by a cambial zone, which has as regards them a normal orientation: by means of it they receive further thickening. Their structure resembles that of the normal *secondary thickening* in the same plant in all important points. Thus spiral vessels are absent here also from the wood. *Almost* simultaneously with the appearance of this second cambium and second ring, the secondary thickening of the first normal ring ceases, at least in carefully investigated cases. In the same way the second may cease to grow, and be replaced by a third like it, and the same process may repeat itself through unlimited series.

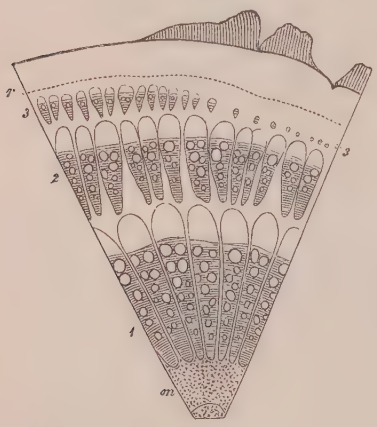

Fig. 233.—Gnetum scandens. Piece of a transverse section of a branch (8); *m* pith; 1, 2, 3, successive rings of growth, the 3rd at the right just beginning to develope, but already strongly developed to the left; *r* ring of stony sclerenchyma, at the inside of the outer cortex, which is covered by fissured cork.—Cortex, medullary rays, and intermediate zones are left white, also the bast-strands, but the latter are limited by a single line; the strands of wood united with them are transversely shaded, excepting the transverse sections of the large pitted vessels.

The successive rings, consisting of wood, bast, and limited cambium (Fig. 233), may, as above, be called shortly rings of growth. They are separated from one another by zones of dissimilar tissue, the special quality of which may vary according

[1] Compare the quoted works of Gaudichaud, A. de Jussieu, Mettenius, Crüger, F. Müller, Bureau; further those to be quoted in this paragraph, by Decaisne, Nägeli, Radlkofer, and Eichler, and in §§ 192–195.

to the special cases to be described. The successive rings may be briefly termed concentric, inasmuch as the separate portions of all have a similar orientation relatively to the organic central point of the whole transverse section of stem or root. This term is not always strictly accurate. There is often strongly eccentric development, or stronger development sometimes on one side, sometimes on another. Not unfrequently instead of a complete ring only portions of one are formed, and these are then often so far eccentric that their margins abut on rings or portions of rings next within them. In flat or winged stems of Lianes, e. g. many Leguminosæ[1], one can in many cases hardly speak of portions of rings at the corners, but rather of parallel striæ or bands.

Since the xylem-portions of the rings usually form the chief mass, as in normal wood, and the bast-portions are relatively small, it follows that, in portions of rings which are very closely packed and short, facing alternately to different sides, and with their margins always fitting closely on the next inner ones, the whole of the xylem portions in the transverse section of stem or root form a connected mass of wood, in which the layers of bast belonging to them, together with the narrow intermediate zones, run as curved, irregularly concentric, and relatively narrow bands. This is very striking, e. g. in the Securidaca figured by Müller (*l. c.* Fig. 6), and the Hippocrateaceous plant Tontelea, represented *l. c.* Fig. 7. Not only in the last-mentioned cases, where the successive portions of rings are in immediate contact at their margins, but also in the cases of more regular concentric arrangement, the radially successive similar zones are in direct continuity, either at the nodes alone, or at numerous points in their longitudinal course.

According to the structure of the individual successive rings, which varies like that of the normal wood, according also to their relative thickness, and that of the intervening zones, according to the special structure of the latter, and the different degrees of concentric arrangement, of length, orientation, curvature, and marginal connection of successive rings and portions of rings, and finally, according to the general form of the transverse section of stem or root, the structure of the parts in question may differ with endless variety. It would lead us too far to enter into all the individual cases which here present themselves. As opportunity offers therefore, single examples may be brought forward, partly in this paragraph, partly in those which treat of Chenopodiaceæ, Phytolacca, and Cycadeæ. Compare also the description of Fig. 227.

As regards the place of origin of the successive renewed zones of growth two different cases must be distinguished.

(1) The more rare mode is this, that zones of growth following the normal one arise in the primary outer cortex. It was discovered by Decaisne[2] in Cocculus laurifolius, and exactly described later by Nägeli[3], Radlkofer[4], and Eichler[5], and occurs generally in the *Menispermeæ* of this category; further it is found in the *Cycadeæ* to be described below, and in the peculiarly constructed stem of the *Avicennias*.

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[1] Compare Crüger, Botan. Zeitung. 1850, Taf. III. Figs. 19–21, Rhynchosia phaseoloides.

[2] Mém. sur les Lardizabalées, Arch. du Muséum d'Hist. Nat. 1 (1839).

[3] Beitr. I. *l. c.*

[4] Flora, 1858, p. 139.

[5] Denksch. d. bot. Ges. Regensburg, Bd. V. p. 1.

In the young branch of *Cocculus laurifolius* the narrow pith is surrounded by a normal ring of wood and bast, as in Menispermum (p. 456), with broad medullary rays, and relatively narrow bundles. Each portion of bast of the latter is limited from the outer cortex by a many-layered half-ring of hard sclerotic fibres. The outer cortex is chiefly parenchymatous, about 7–9 layers of cells thick, including the epidermis, and without special peculiarities. The normal growth in thickness of the first zone of wood and bast continues, as far as is known, for 1–2 years. Then the activity of the cambium ceases. A radial extension now begins in the 2–3 inner layers of parenchyma of the outer cortex, followed by tangential divisions, the latter proceeding especially, though not exclusively, in a centripetal direction. The thickness of the parenchymatous cortex thus increases to 18–20 layers of cells. Of these the 10–11 outer ones remain unaltered: 3–4 layers next within these become hard stony elements, forming a continuous ring. Inwards from this ring the tangential divisions continue, especially in centrifugal progression. Some of the inner layer of cells thus formed pass over into the condition of permanent very thick-walled parenchymatous cells; they form a continuous zone surrounding the exterior of the primary strands of bast-fibres; into this the primary medullary rays, which resemble it in structure, are directly continued. Outside this layer there remains a ring of meristem at first only 1–2 layers of cells thick, in which the second thickening ring is now differentiated. The structure of this is in all respects very similar to that of the first; but its bast-bundles, which are almost semicircular in transverse section, have no fibrous sheath. After the cambiogenetic increase of the second ring has continued for a time, the activity of its cambium ceases; between the outer limit of its bast and the stony ring appears a new thickening ring of the same sort as the second, and so successively onwards.

The figure 233 gives a diagrammatic view of the real appearance of the transverse section of the stem described, and of its congeners, though the representation is not exact since it is taken from another plant.

In the structure of the stem of the *Avicennias* (A. officinalis, nitida, tomentosa) the soft bast and cambium were not clear in the dry material at my command, I therefore limit myself to short notes. The first normal ring of thickening surrounds a wide pith: its irregularly undulating outer margin is marked off by a ring of bast fibres, which shows but few interruptions, from the usually delicate parenchymatous outer cortex, which contains scattered, short, and elongated sclerenchymatous elements. The wood shows a normal Dicotyledonous structure, and is arranged in very regular radial rows. The usually pluriseriate medullary rays consist of rather thick-walled cells, and are continuous with this structure at many places as far as the ring of bast sclerenchyma. Thus as thick-walled bands they divide up the bast zone, which consists for the most part of very delicate elements with isolated fibres scattered here and there, into well-marked sections of unequal size. The first ring hardly attains a thickness of $\frac{1}{3}^{mm}$. Then follows a second ring of thickening, which abuts directly within on the above-mentioned fibrous zone, and is limited externally by a zone of sclerenchyma on an average 1–2 layers thick, the elements of which resemble those of the fibrous zone in transverse section, but are shorter than they. To this zone a third, and then numerous successive thickening rings are added, always in the same manner. The later ones also remain narrow; in a branch 5^{cm} thick for instance they are not on the average thicker than $0{\cdot}5^{mm}$.

The structure of all successive rings is just like that of the first: also the interruption of the soft bast by thick-walled radial bands always takes place, and in such a way that it is effected not only by medullary rays, but here and there by strands of wood, with few vessels, which extend to the outer ring of sclerenchyma. The soft bast is often broken up into single strands which resemble the strands of sieve-tubes of Strychnos. At the time when the youngest ring appears the growth in thickness of the next inner one has in each case already ceased. As regards the origin of the rings it was only possible to make out that a zone of meristem appears outside the sclerenchymatous limit of the last mature ring, in the delicate parenchyma of the outer cortex. When this zone is still

very narrow, and at most only some few cells wide, the sclerenchymatous ring appears at its outer margin, and then within it the beginnings of bundles and medullary rays, and of the cambial zone between wood and bast. The outer ring of sclerenchyma is pushed outwards by the growth in thickness derived from the latter. The often-mentioned thick-walled interruptions of the bast zone can hardly be derived otherwise than by the ultimate conversion of cells of the cambium into thick-walled permanent elements.

(2) In the large majority of cases, the bast-zone itself is the place of origin of the successive rings of thickening; that is, either its outermost (primary) region, as e. g. in Phytolacca, or the outer, older zones of the secondary bast: thus, e. g. in Wistaria chinensis, in stems of Lianes passing under the name Bauhinia, and others corresponding to the Leguminous plant called by Crüger Rhynchosia phaseoloides: further, in the Liane above-mentioned, represented by Müller (*l. c.* Fig. 6) as Securidaca, and (Fig. 7) as Tontelea (?). The same holds for Gnetum, at least for that form represented in Fig. 233, for Phytocrene, Fig. 227, according to Eichler for Doliocarpus Rolandri, and also for those cases to be mentioned directly, which have not yet been carefully investigated in connection with the question under discussion.

The examples cited show that these phenomena belong to very different families, and occur in plants and parts of plants adapted to very different modes of life. In the first place they appear with a remarkable frequency in stems of Lianes, and more especially at least in twining stems, not in those which climb with tendrils, as in Wistaria, Mucuna sp. (F. Müller), and other Leguminosæ already quoted; in Comesperma and Securidaca volubilis from the Polygalaceæ; in Tontelea sp. (Hippocrateaceæ); Cocculus, species of Cissampelos and other Menispermaceæ[1]; Doliocarpus and other Dilleniaceæ[2]; Phytocrene, Gnetum; rarely also in Aristolochias, as shown by Fig. 219, taken from Schleiden's Grundzüge, see p. 550. Lianes with tendrils are not however sharply excluded from such structure as that under discussion, as shown by old stems of the Sapindaceous genus Thinouia (p. 583), and the Bignoniaceous plants Haplolophium and Glaziovia (p. 575). Also the solitary cortical bundles, which A. de Jussieu describes in Anisostichus capreolata, may belong to this category. On the other hand, it is to be noted that stems of Lianes, which are closely related to the species here mentioned, such as Menispermum canadense, and most climbing Aristolochias have no renewed zones. And I may further mention the appearance of the latter not only in the stem of the non-climbing Menispermaceous plant Cocculus laurifolius, but also in others, as far removed as possible from being climbing forms, such as the Avicennias mentioned above, Phytolacca, and Cycadeæ, to which may be further added Mærua uniflora (of the Capparidaceæ) from East Africa, with a stem structure like that of the above-mentioned Tontelea. In some Lianes, Wistaria, Menispermeæ, and Securidaca volubilis (Crüger), the structure and course of growth described extends also to the roots; most of them have not been investigated on this point. On the other hand, it is found, as far as is known, as a general family-character in the roots of species of Phytolacca, Chenopodiaceæ, Amarantaceæ, &c., even if the stem shows another character. Comp. Sect. 192.

We shall return in Sect. 194 to the phenomena of growth of the roots of Convolvulaceæ, which also belong to some extent to this category.

[1] Eichler, *l. c.*, and in Flora brasiliensis, Fasc. 38, p. 207, Taf. 50, 51.

[2] Crüger, *l. c.*—Eichler, in Flora brasiliensis, Fasc. 31, p. 116.

Sect. 192. The families of the *Chenopodiaceæ*, *Amarantaceæ*, *Nyctagineæ*, *Mesembryanthema*, and according to Regnault also the *Tetragonieæ*, and as far as is known all their congeners, show a series of anomalies of growth and structure, corresponding in certain main features, but with various differences in detail within the same family and even the same genus. With these may be connected *Phytolacca* among the Phytolaccaceæ, while in the genus *Rivina* (R. brasiliensis and aurantiaca), placed in this family, the stem and root have normal growth and thickening[1].

The common peculiarity of structure of the parts in question consists in the fact that the secondary thickening, within the annular active cambium zone, contains more than one circle of distinct collateral vascular bundles showing a limited growth: these are embedded in unlike tissue, which may be generally termed *interfascicular* or *intermediate tissue*.

This structure, in its individual forms, originates in different ways.

1. A primary ring of bundles appears in the stem, and in the roots the primary axile bundle: in both there is first a normal cambium with normal products. The activity of the latter then ceases, and around it appear in centrifugal order successively renewed and disappearing cambiums, each of which forms a circle of distinct vascular bundles. This mode occurs in all investigated roots of plants of this category with the exception of those to be named under (3); further, in the stem of Phytolacca, and, judging from Regnault's statements, which require corroboration, also of Tetragonia and Sesuvium; according to the individual case the successive rings are variously complete and regular.

2. In a number of stems there is at first a primary ring of bundles, consisting of leaf-trace bundles, and often perhaps of intercalary bundles also (p. 456); in species of Amarantus (p. 249) there are also medullary leaf-traces. While the development of the collateral bundles is still proceeding there appears *round the outer margins* of their phloems a *ring of cambium*, which is accordingly *extrafascicular*; this remains *permanently* active, and forms on its inner side alternately collateral vascular bundles and intermediate tissue, on its outer side a thin layer of bast, consisting only of parenchyma, or even no bast at all. This is the case in the investigated stems of shrubby Mesembryanthema, the stalks or stems of Mirabilis, Oxybaphus, and of all Nyctagineæ (Pisonia, Boerhavia, Bougainvillea, Neea); of

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[1] Literature:—*Chenopodiaceæ*. Unger, Dicotyledonenstamm, *l. c.*, p. 260.—Von Gernet, Ueber den Bau des Holzkörpers einiger Chenopodiac., Bull. Soc. Imp. de Moscou, 1859, I. p. 164. There is there quoted: Basiner, in von Baer and Helmersen, Beitr. z. Kenntn. d. Russ. Reichs, Bd. XV.—Sanio, Botan. Zeitg. 1863, p. 410; 1864, p. 225.—Regnault, in Ann. Sc. Nat. 4 sér. tom. XIV. (1860).

Amarantaceæ. Link, Elem. Phil. Botan. ed. 2, p. 444.—Unger, Regnault, *l. c.*—Sanio, Botan. Zeitg. 1864, p. 229.

Nyctagineæ. E. Meyer, de Houttuynia, p. 40.—Unger, Regnault, *l. c.*—Nägeli, Beitr. I. p. 119.—Sanio, *l. c.* 1865, p. 197.—Finger, Anatomie u. Entw. von Mirabilis Jalapa, Diss. Bonn. 1873.—Grönlund, Stammens og Grenens anatom. Bygning hos Neea theifera sammenholdt med andre Nyctagineer. Vidensk. Meddelels. nat. Forening Kjöbenhavn, 1872, p. 60.

Mesembryanthemum. Regnault, *l. c.*—Falkenberg, in Göttinger gel. Anzeigen, 1876, p. 99. Botan. Zeitg. 1876, p. 317. [Also Petersen, Bot. Ztg. 1878, p. 785.]

Phytolacca. Martins, Revue horticole, 1855, p. 123 (Botan. Zeitg. 1856, p. 582).—Treviranus, Botan. Zeitg. 1856, p. 833.—Regnault, *l. c.*—Nägeli, Beitr. *l. c.* pp. 26, 118.

Amarantus retroflexus, Celosia argentea, Alternanthera Verschaffeltii (Amarantaceæ); of Chenopodium album, Atriplex patula, and Salicornia herbacea.

Between these two chief modes or types the following are intermediate.

3. In the root of Mirabilis the phenomena of secondary thickening are the same as in 1. as far as the appearance of the first renewed zone of cambium. This then remains permanently extrafascicular and active according to mode 2. The same behaviour appears to occur in the roots of Oxybaphus; those of other Nyctagineæ have not been investigated.

4. The stems of many Chenopodiaceæ, as Ch. hybridum, Ch. murale, connect types 1 and 2, since a normal cambium and a normal secondary thickening appears as in 1 in their primary ring of bundles; this however soon stops, and the further growth in thickness is continued, according to mode 2, by a new extrafascicular zone of cambium, which appears outside the primary masses of phloem. Blitum virgatum, Gomphrena decumbens and globosa, and Frœlichia gracilis behave in this way; their slightly thickened herbaceous stems show for a long time only a quite normal thickening, the bundles situated outside the ring of bast appear in small numbers, or often not at all.

The relation between 1 and 4 being very close, it is impossible to distinguish in the old stem whether the first stages of thickening proceed according to the one or the other type. Therefore in the case of Atriplex Halimus, Obione sp., Salsola kali, Arthrocnemum fruticosum, Haloxylon ammodendron, Caroxylon arbuscula, Alternanthera spinosa, Ærva javanica, Achyranthes aspera, Pupalia Schimperiana, and according to Regnault's statements in the Tetragonieæ Galenia, Trianthema, and Tetragonella, of which the first stages were not investigated, it can only be said that they certainly belong to one of the two types.

This is the proper place to insert a remark upon the terms which have been, and ought to be employed. According to the terminology which is usual, and has been adopted in the preceding chapters, each thickening zone with normal orientation and structure is to be denominated, even in the cases before us, respectively *cambium*, *wood*, *bast*, &c., and there is no difficulty in applying these terms to successively renewed and arrested annular zones. But in those cases (2) in which the orientation of the meristematic layer, which brings about the secondary thickening, is from the first other than normal, the adoption of the terminology used in other cases may be questioned. Even if intermediate forms were not present, it is suitable in all cases to call the initial layer of each secondary thickening here also generally cambium, especially as—leaving out of account special differences which still remain to be investigated—this layer always possesses in itself the other fundamental properties of normally arranged cambium. Since a special name is desired for the special orientation indicated under 2, the term *extrafascicular* has been chosen for such cambium as appears outside the primary ring of bundles. Starting from the above reflections we must consistently apply the term *wood* in the cases of extrafascicular cambium also to the secondary thickening, whenever it appears on the inner side of the cambium, and in centrifugal succession, and the term *bast* to that which appears centripetally on the outside. The bast differs here as in Strychnos from normal bast in its structure, as does the wood also, reminding one of the phenomena described in Strychnos and Dicella. Link calls this wood *lignum hybridum*, bastard-wood; but it may be more satisfactory to give up the use of this remarkable name, which was accepted even by Sanio, and to describe precisely in each instance the real state of the case, since it is subject to such indefinite variation according to the individual instance.

The structure of the individual zones of thickening has, with the exception of some few cases to be rather more accurately described below, been very incompletely studied, and further investigations are the more to be recommended, since very numerous differences appear in the special phenomena, at all events in different species and genera. What follows can but give some indications of this.

As has been already stated above, the structure of each *zone of cambium* and the succession and direction of the divisions in it are in general, and with the exception of individual characters still to be ascertained, the same as in normal cambiums. The same holds for the originally radial direction, and the subsequent displacements of the mother-cells of tissues or elements successively derived from the cambial layers. For cases of extrafascicular cambium it may be added to these statements in the first place that the latter is always derived, as far as investigated, from tangential division of a single layer of parenchyma or meristem in contact with the outer margins of the masses of primary phloem. The secondary thickening by cambium begins while the differentiation and extension of the tissues surrounded by it proceeds, and *especially the leaf-trace bundles may continue to grow by formation of new elements* at the limit between xylem and phloem, after the manner of collateral bundles (comp. p. 390). Longitudinal divisions of the cambial cells proceeding in centrifugal succession add radially arranged secondary elements to the primary ones; most of them pass over directly, or at most after a single further longitudinal division, into definitive tissue-elements, and are thus young wood-elements, or the direct mother-cells of these. In this manner arise the elements of interfascicular tissue, in many cases also those of the xylem of the bundles. But at certain points in the ring of cambium there appear directly in one or a few tissue-mother-cells lying close together, and separated off internally from the ring itself, rapidly repeated longitudinal divisions facing in all directions; these form an initial strand (comp. Sect. 115) from which, in the manner described generally for the collateral bundles, either a whole vascular bundle is derived, or the phloem of a vascular bundle, the xylem of which had already been begun by the simple tangential divisions in centrifugal succession. In both cases the simple centrifugal tangential division proceeds further outside the initial bundles; outside each one of these interfascicular tissue is again formed, and the same process repeats itself as the cambial ring is removed from the centre; it is repeated in the same transverse section successively on different radii, and in successive transverse sections with such an arrangement of the initial bundles, that the longitudinal course of the bundles, to be subsequently described, is brought about. In the initial bundle, however, or the vascular bundle derived from it, the growth is usually continued, when the increase at its outer margin has already ceased. Tangential divisions are often found at the limiting surface between phloem and xylem of a bundle, when the cambial ring is already separated from its outer margin by several layers of cells in which division has ceased.

In addition to the centrifugally formed fresh derivatives of the cambium there are usually also centripetal formations, that is, a formation of bast: thus, e. g. in shrubby Mesembryanthema, species of Obione, Halimus, &c. But in many cases, as in the first internodes of the seedling of Chenopodium album, and Mirabilis Jalapa, I have remained in doubt as to the appearance of centripetal divisions.

Wood and *bast* consist, as has been stated, of collateral vascular bundles, and

intermediate tissue. The arrangement of the latter is, at least in extreme cases, different according to the presence of successively renewed rings of cambium and thickening, or of a permanent extrafascicular cambium.

In the first case the bundles are arranged like the strands of wood or bast of a normal Dicotyledonous ring. One strand of bast corresponds to each strand of wood, the two together forming one collateral vascular bundle. Between two bundles of a ring lies a radial band of intermediate tissue, which, with reference to the ring itself, is like a normal medullary ray; each pair of successive rings is divided by a zone of intermediate tissue. As will be shown below by examples, these zones derive their origin from the outer margin of the zone of bast bordering them internally, or the parenchyma directly adjoining this margin externally. The bundles of successive rings are connected one with another by branches with an obliquely radial course, the arrangement of which varies according to individual cases to be described below. The number of the successively alternating zones of bundles and intermediate tissue has no constant relation to that of the annual periods of growth, but rather in one period of vegetation a number of successive zones without definite limit are formed.

In the second case all bundles lie in the wood, and alternate both in radial and tangential direction with intermediate tissue, either so that they appear in a transverse section distributed quite irregularly in the latter, as e. g. in the thick masses of wood of shrubby and tree-like Chenopodiaceæ (Halimus, Arthrocnemum), Nyctagineæ (Bougainvillea, Pisonia[1]), Amarantaceæ (Aerva, Pupalia[2]), and Mesembryanthema; or that they appear in a transverse section arranged in irregularly concentric zones within the intermediate tissue, as in Salsola, Haloxylon, and Caroxylon; in the root, and partly also in the stems of Mirabilis. It is doubtful how far these zones are related to the annual production in woody stems; in Mirabilis there is no such relation. In their longitudinal course the bundles show mutual connections both in a radial and tangential direction; in the stem of Mirabilis these are at the nodes; in the other investigated cases also at other points, since, in their course, which undulates in both directions, they alternately approach and recede from one another, thus forming elongated and pointed meshes.

The histological composition of the vascular bundles is in general like that of collateral bundles, with the limitation that narrow spiral and annular vessels are usually restricted to the bundles of the leaf-trace; only the inmost, apparently medullary secondary bundles of Mirabilis and other Nyctagineæ have, like these, spiral vessels also. In the other secondary bundles the xylem consists of pitted vessels, and in sappy and fleshy parts also of reticulate vessels, and of parenchymatous and fibrous elements which require further investigation. Between the two latter the vessels are arranged usually in one or a few, more or less regular radial rows; more rarely one or another vessel is at a distance from the rest in the intermediate tissue. In many Mesembryanthema the arrangement seems to be less regular, so that the vessels appear 'irregularly scattered' in the intermediate tissue[3]. The phloem in

[1] [See Petersen, z. Hist. u. Entw. des Stengels der Nyctagineen, *Ref.* Botan. Zeitg. 1880, p. 509.]

[2] Under the generic names quoted it is intended in each case to include specially the above-named species belonging to them.

[3] Compare Falkenberg, *l. c.*

the stem of Phytolacca has the structure of perfectly typical soft bast; in the other investigated cases there is usually a great preponderance of parenchyma, with only very narrow and isolated sieve-tubes. These may therefore be easily overlooked, and are to be further investigated; where I examined them carefully (Mesembryanthemum, Atriplex sp.) they had the typical structure. In all cases the elements of the phloem are united to a narrowly circumscribed group, and not scattered over a wide area. Sclerenchymatous fibres have not been found in the secondary phloem in any case investigated.

The intermediate tissue appears in extreme cases in two different forms, namely as thin-walled large-celled parenchyma, or as sclerotic spindle-shaped woody fibres. The former is in all cases sappy, rich in products of assimilation, and often shows an independent growth, which is long continued even at a great distance from the cambium: this growth is connected with cell divisions, and exercises an important influence upon the whole structure. Intermediate forms between the two named, such as thick-walled 'xylem parenchyma,' &c., are not wanting, but require more exact investigation. The latter remark applies also to the distribution of both forms. If only the most fundamental phenomena be taken into account, the following rules may be applied to the occurrence of the two kinds of tissue:—

(1) All intermediate tissue consists of delicate, large-celled parenchyma, rich in products of assimilation. Fibrous elements do not occur at all (root of Mirabilis), or only in immediate company with the vessels, that is, as constituents of the strands. This is the case in most fleshy roots of this category, e. g. Beta, and in the stem of Phytolacca dioica.

(2) The intermediate tissue consists both of parenchyma and of elongated, spindle-shaped, sclerotic, fibrous elements; this is the case in—

(*a*) The extremely hard woods of the shrubs and small trees of the steppes, of the genera Halimus, Caroxylon, Haloxylon, &c., and the tougher stems of other Chenopodiaceæ, Amarantaceæ, Nyctagineæ, and Mesembryanthema, the chief and fundamental part of which consists of the latter; parenchyma appears to be distributed among it in small groups, like the bundle-parenchyma of normal wood, but this requires more exact investigation. It is often found in radial bands of various size; but most especially, almost always, in several layers surrounding the phloem portions of the vascular bundles externally and laterally. Where the latter are arranged in concentric zones, it thus forms zones of parenchyma, or consisting mainly of parenchyma. The cells of this parenchyma which accompanies the bundles are sometimes, like those of the ordinary fascicular parenchyma of firm normal woods, very thick-walled, and pitted; but in most cases the layers immediately surrounding the phloem remain thin-walled and sappy. Like the phloem-strands of Strychnos, they with the groups of phloem fill up spaces in the hard mass of xylem, which are round or oblong in transverse section, and which in dry woods are usually for the most part empty by reason of the shrinking of the delicate tissue. I have only rarely found exceptions to this, e. g. in the Salsola investigated. As far as investigation extends, all the elements mentioned are arranged radially with considerable regularity in the firmer woods in question. Grönlund states that there are numerous medullary rays in the wood of Neea.

(*b*) Those cases are but little worthy of remark, in which both thin-walled

parenchyma and hard fibrous elements form large masses, which appear in transverse section as alternating, irregular, concentric zones or islands; this arrangement occurs e. g. in Chenopodium hybridum, and, according to Falkenberg, in many Mesembryanthema.

(*c*) The intermediate tissue formed at the beginning of the activity of the cambium assumes in many cases an exclusively parenchymatous nature where the cambium is extrafascicular; its cells are more or less displaced from their radial arrangement, by reason of the more continued strong extension of the masses of tissue surrounded by them, and their own considerable growth in the transverse direction. They are therefore arranged similarly to those of the primary pith, and further they remain thin-walled like the latter and those of the primary medullary rays, and therefore form with these two parts a connected mass of wide and delicate cells. Later, when the transverse extension of the pith and the tissues near it ceases, the pith-like intermediate tissue is succeeded by a dense tissue, with structure and arrangement similar to (*a*). Since the latter together with the vascular bundles enclosed in it correspond to the usual appearance of dense 'wood,' it alone appears in transverse section to represent the ring of wood, while the wide-celled internal tissues surrounded by it, including both primary and secondary bundles, appear one and all to be medullary. Such *apparently medullary* bundles are to be distinguished from true medullary bundles, i. e. such as are within the primary ring of bundles (comp. p. 248). Their occurrence appears to be not uncommon in the plants in question, and is subject to two chief modifications. In the first place, a number of layers of pith-like intermediate tissue are formed outside the primary ring of bundles, but between the secondary bundles only dense tissue; the primary ring alone appears to be medullary in this case—and further is often very near to the dense secondary ring. Thus, e. g. in Chenopodium album, Atriplex patula, Celosia, and Achyranthes; in species of Amarantus there are also true medullary bundles of the leaf-trace. In other cases pith-like tissue appears also between the inner secondary bundles, so that the transverse section shows in addition to the primary ring also one or several, apparently medullary rings of bundles, as in the stem of Mirabilis, Oxybaphus, and also other Nyctagineæ.

All that is necessary has already been said above about the structure of the *bast* in the forms with successively renewed annular zones, for here, if the expression be allowed, each annular zone has its own layer of bast. For the other forms it may be again stated that the secondary layer of bast, when present at all, consists, as far as investigated, only of relatively few layers of radially arranged parenchyma, in which crystal-containing sacs are not unfrequently scattered. Bast fibres are found, scattered or forming a dense ring, only at the outer limit of the primary bast-layer of the stem, and are absent even there in many species; in the secondary bast they are found in none of the plants under consideration.

To illustrate the above, two or three examples may be more thoroughly described, though space does not here allow of an exhaustive description of the somewhat complicated phenomena.

1. Firstly, the shrubby *Mesembryanthema*. I have specially in view a form named as M. virens Haw. Other species resemble this, in the main, according to the notes of Regnault and Falkenberg, while in others again, as the annual M. crystallinum, greater

variations appear to occur. The leaves are arranged in decussating pairs. The course of the bundles of the leaf-trace, which is certainly very simple, has not been exactly investigated. In the young, and but slightly extended internode they are disposed round a narrow pith in a ring, which is in transverse section somewhat bluntly rectangular. The two shorter sides of the rectangle are occupied by the bundles belonging to the next higher pair of leaves, the two longer ones by those which descend from higher leaves. The bundles are collateral. Their phloem portions are surrounded by a zone of narrow thick-walled collenchymatous elements, which is several layers of cells thick, and runs round the whole ring: this zone is bordered externally by the thick large-celled outer cortex, traversed by the network of bundles mentioned on p. 297. The innermost limiting layer of this (Pierome-sheath) is developed as a starch layer (comp. p. 415). Before the development of the bundles of the leaf-trace is complete, tangential cambial divisions begin in an outer layer (but not the outermost) of the zone of collenchyma: thus they are extrafascicular. As far as I could see they begin first on the long sides, then on the short sides of the rectangle, and are then continued from these four starting-points over a completely circumferential layer of cells. The tangential divisions and the arrangement of their products in radial rows are from the first very regular, and remain so, since the latter and the cambium always uniformly follow the slight expansion of the internal parts. Externally to the circle of the leaf-trace, in the first place a zone many layers in thickness is formed, consisting of radially-arranged interfascicular tissue—in M. virens of sclerotic elements. Further outwards the vascular bundles appear in the intermediate tissue, which becomes sclerotic with the exception of the thin-walled portion surrounding the phloem; in the transverse section these bundles are arranged in interrupted and irregular concentric annular zones, which are often interlocked one with another. The vessels of the bundles are at least for the most part derived directly from simple cambial tangential divisions. When the xylem of a bundle has been thus formed, an initial strand is added at its outer side, from the active divisions of which the delicate phloem is produced; I am not able to say whether the outermost vessels of the bundle are also thus formed or not. Centripetal divisions of the cambium, the succession of which has not been exactly traced, produce in M. virens a secondary layer of bast composed of radially seriate, elongated parenchymatous cells. In stems, in which the radial rows of the secondary wood numbered over fifty elements, there were only five cells in one radial row of the bast. After the extension of the internode is complete, and before the first ring of secondary vascular bundles is formed, the thick outer cortex is thrown off by a formation of periderm, which starts from the starch-layer; the layer of cork cells thus derived is several layers thick over the broad sides of the ring of bundles, being formed by tangential division of the starch-layer; over the narrow sides, however, it is for certain distances a single layer, and arises apparently directly by suberisation of the starch-layer, without previous divisions.

The roots of the Mesembryanthema have not been investigated in detail.

2. From each of the leaves arranged in opposite and decussating pairs on the foliage shoots of *Mirabilis Jalapa* and *longifolia* (Figs. 234, 235) three bundles of the trace enter the stem, one median (*m*), and two lateral (*l*). They traverse the internode with a radially perpendicular course, and at the next lower node each trace unites to form a single bundle (*v*); this projects rather deeper into the pith, and passes perpendicularly down the next node, inserting itself at the second lower node on the traces, which there join into a single bundle; it curves first to one side and is affixed to one of them, and then by a second shank, which appears later, it is joined to the one on the other side. The transverse section of a young internode (see Fig. 235) therefore shows first eight bundles, ranged round a prismatic pith: on each side, corresponding to the next higher pair of leaves, are the three bundles of the trace of the leaf above it, and alternating with these two traces, but rather nearer the centre, are the opposite united bundles from the pair of leaves next but one higher. Somewhat later new bundles appear in the internode outside the eight bundles of the ring, and at the same time a ring of meristem, the

extrafascicular cambial ring (*c*), which is somewhat more external, and consists for the most part of a single layer, becomes visible: it is sharply distinguished from the parenchyma in- and outside it (which has meanwhile become large-celled) by the small size of the transverse section of its cells. If we first consider the longitudinal course of the new bundles, which become visible at the same time as the cambial ring, and of those which appear rather later and will be treated of subsequently (Fig. 234 *a*), they pass perpendicularly through the internode, being arranged in one or two circles outside the bundles of the leaf-trace, and without any quite definite position relatively to the latter. In the node limiting the internode above and below they are inserted on the outgoing lateral bundles of the trace, and are also connected at once one with another by a curved transverse anastomosis. Later, this insertion is obscured by the appearance of very numerous connecting branches at the node.

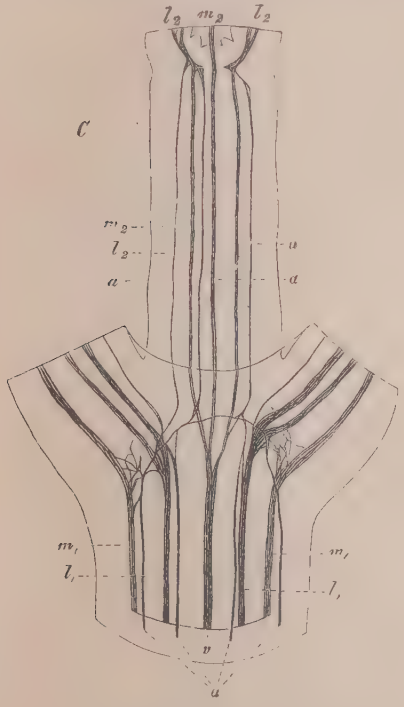

Fig. 234.

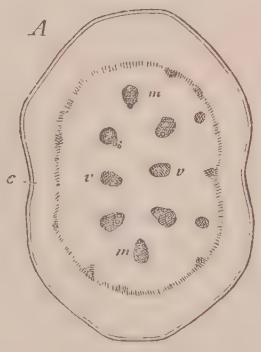

Fig. 235.

FIG. 234.—Mirabilis Jalapa. Seedling, first and second epicotyledonary nodes; above the latter is the growing point with the third pair of leaves just beginning to appear, and seen through the base of the leaf which is opposite the observer. The preparation was made transparent by potash and glycerine, and consists of one longitudinal half, seen from *without*, and with the vascular bundles drawn in. m_1 median bundles of the leaves of the first pair; m_2 median bundle of the nearer leaf of the second pair; l_1, l_2 lateral bundles of the trace of the first and second pairs of leaves; *v* united bundle of the trace; *a*, *a* secondary, apparently medullary bundles.

FIG. 235.—Mirabilis Jalapa. Transverse section through the young first epicotyledonary internode (40). *m* median bundles, *v* united bundles of the leaf-traces passing through the internode; between *m* and *v* on either side are two lateral bundles; *c* extrafascicular cambium; the extensions of this protruding inwards are initial secondary bundles; two of the latter are separated from the cambium by a layer of parenchyma (left white).

The first one or two of these bundles, which are outside the leaf-traces, always became visible as young initial bundles at the same time as the cambium, but were separated from it by a narrow zone of parenchyma: it can hardly be doubted that they, like those which are subsequently formed, are really derived from the cambium. As soon as the ring of cambium is clearly seen, successive new initial bundles are formed in it, which

develope into the bundles arranged round the leaf-traces. One, and perhaps some few closely grouped cells of the cambial ring divide tangentially; from the internal cell or cells an initial strand is formed by longitudinal divisions facing in different directions, while the outer cells continue the centrifugal tangential division. Those products of the latter, which adjoin the initial strand externally, assume at once the properties of relatively wide parenchymatous cells, the initial strand is therefore separated by parenchyma from the cambial ring, which successively retreats outwards.

Simultaneously with the first formation of the initial strands, a centrifugally successive development of parenchyma on the part of the cambium takes place between them. Since this development continues slowly, the cambial ring, which retreats slowly outwards, forms a number of new initial strands in the manner above described, at successively alternating points at its periphery; this centrifugally progressive activity accordingly produces those irregular circles of vascular bundles, separated by delicate and wide-celled parenchyma, which surround the ring of the leaf-traces. The number of these bundles varies greatly according to the strength of the internodes; in weak seedlings it is often hardly 8–10 (Fig. 236), in strong flowering shoots 2–3 times that number. During the process described, the growth in the direction of the transverse diameter continues in the middle of the transverse section of the internode. The vascular bundles increase the number and size of their elements in the usual way — especially the united bundles of the trace (*v*) are usually to be distinguished at an early stage by their considerable size; the cells of the whole interfascicular parenchyma increase throughout in width. The cells derived directly from the cambium must therefore be displaced from their original radial direction, and the more so since the cambial divisions apparently succeed one another relatively slowly. Even the cells of the cambial ring itself often show an irregularly distorted arrangement. Finally, a stage is arrived at, in which the extension of the inner parenchyma ceases, and simultaneously the cell divisions in the cambium succeed more quickly and in greater number without changing their succession. Thus a ring of thickening is now formed, which consists of relatively narrow elements, arranged in regular radial rows; it is composed, on the one hand, of a fundamental mass of sclerotic elongated cells, on the other, of vascular bundles embedded in this fundamental mass; for the origin and arrangement of these, fundamentally the same may be said (that is, if details be not taken into account) as above for Mesembryanthemum. The old internode thus shows apparently medullary bundles within a dense woody ring (Fig. 236).

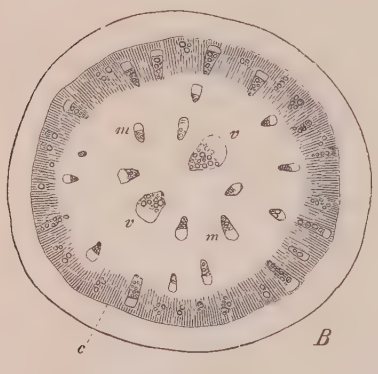

FIG. 236.—Mirabilis Jalapa. Transverse section through the first epicotyledonary internode of a young specimen, which is already several internodes in height (15); *v* and *m* as in Fig. 235, next to *m* are the lateral bundles; round the eight bundles of the trace are nine apparently medullary bundles in the parenchyma, which is left white; further outwards is the thick ring of wood; *c* cambial-zone.

In the thin first internodes of the main stem of seedlings I first saw no bast parenchyma derived externally from the cambium. Later this process may begin, and in strong plants this is always or as a rule the case. Similar, but simpler conditions occur, according to Nägeli's description, in *Pisonia hirtella;* also the more complicated phenomena which Nägeli describes in the internode of *Boerhavia scandens* and *Bougainvillea spectabilis* are to be connected with the above.

The growth in thickness of the root of Mirabilis begins like that in normal Dicotyledons. Comp. p. 473. The vascular strand is rarely tetrarch[1], usually triarch; the

[1] Van Tieghem, Symmétrie de structure, *l. c.*, compare p. 473.

latter case only will be here taken into account. Opposite each face of the vascular plate a strand of wood and bast containing much parenchyma is formed in the normal way, and before each angle a broad primary medullary ray. In the pericambium a periderm begins simultaneously to be formed, and by it the outer cortex is thrown off. The primary medullary ray consists exclusively, and the bast mainly, of radially seriate parenchymatous cells, which gradually become greatly elongated in the same direction: these together form a thick layer inside the periderm. In the peripheral portions of this layer, near to the phellogenetic zone of the periderm, tangential division begins all round, at the time when the root begins to swell strongly, and thereby a fresh (renewed) cambium is started. The formative activity of the first normal layer now falls off, and soon ceases altogether. The second cambium alone continues the secondary thickening of the root throughout life. By means of tangential divisions proceeding for the most part centrifugally, it forms alternately radially arranged parenchyma and vascular bundles. The latter are connected in radial and tangential direction in acute-angled meshes, and are arranged in the transverse section in tolerably regular annular zones, which alternate with zones having no bundles, and differ from the latter also by the less marked radial extension of the parenchyma; they are thus very conspicuous.

Fundamentally the same phenomena of thickening appear in the hypocotyledonary portion of the stem, which takes part in the turnip-shaped thickening of the main root: the peculiarities of this part are irrelevant, and may pass unnoticed here[1].

3. In the root of the cultivated forms of *Beta*[2], a diarch primary vascular bundle was always found in the cases investigated: the secondary thickening begins fundamentally in the same way as in Mirabilis, and proceeds for a time in a normal manner. The cortical parenchyma surrounding the outer margin of the primary groups of bast thus becomes much thicker opposite the two secondary bundles than opposite the angles of the primary vascular plate; I will not say for certain whether this is the result, as stated by van Tieghem, of a formation of phelloderm, starting from the pericambium which acts as a phellogenetic layer, or of active growth of the parenchymatous elements of the primary bast (i.e. of the primary phloem strands) seated within the pericambium. After a time, in the case of the main root of B. vulgaris when it is about $\frac{1}{2}^{mm}$ thick, the formation of a new cambial zone starts in this peripheral layer of parenchyma on both sides, by regular successive tangential divisions appearing in an annular layer of cells. Since this process is continued, from the middle of the two points indicated, laterally towards and over the two main medullary rays, a completely closed cambial zone is formed, which undergoes active reciprocal tangential division: in it are differentiated strands of wood, and of bast corresponding to them, and medullary rays, which are further developed after the manner of normal secondary thickening. Later, the growth of this second thickening zone ceases, and it is replaced by a new one similar to it, which had already begun to appear at the outer limit of the chiefly parenchymatous second layer of bast, in the form of tangential divisions, which arise at scattered points, and extend thence laterally all round. Since the same process is repeated, there arise in the Beet those well-known concentric rings of wood, broken up by medullary rays, which alternate regularly with the chiefly parenchymatous zones of bast, the number of which may be as many as six and more in a strong one-year-old beet. According as the rings are further from the centre, and therefore wider, the number of their strands of wood and bast increases.

Between the bundles of successive rings there are obliquely descending radial connecting-bundles. Further, instead of a ring, larger or smaller segments of a ring may appear here and there, which are then connected by their margins to the next inner rings. Here also the hypocotyledonary axis takes part in the formation of the beet, the phenomena being similar to those in the main root.

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[1] Compare van Tieghem, *l. c.*

[2] [See Droysen, Beitr. z. Anat. u. Entw. d. Zuckerrübe, Halle, 1877.]

In addition to the phenomena of secondary cambial formation above described, there occurs in the Beet the above-mentioned phenomenon of growth of the older parenchyma, even at a distance from the active cambium: this process influences the definitive structure. Even in young roots, in which the formation of the innermost zone of increase has begun, it may not unfrequently be seen that the connecting cells (comp. p. 351), which separate the primary plate of xylem from the secondary strands of wood, are transversely extended, divide, and thus give rise to a band of parenchyma, which intervenes between the strands of secondary wood and the primary plate, and separates the two parts one from another. This phenomenon may appear on both or only one face of the plates. With the further growth of the root the intervening band may increase to a width of 2^{mm}. It is continuous externally into the *simultaneously growing* parenchyma around it, especially of the chief medullary rays. Also the other internal parenchyma, both that belonging to the xylem and that which forms the greater part of the zones of bast, has a growth accompanied by slow cell division, and continuing long after the appearance of the next outer cambial ring: the limits of this growth have not been exactly ascertained. In consequence of the growth of the zones of bast in a radial direction, the successive rings of wood are separated more and more from one another; and the increase in volume of the parenchyma in the individual ring of wood separates the non-parenchymatous elements of it one from another, both in the direction of the radius and of the periphery; especially the meshes, which are formed by the bundles, are widened by dilatation of the medullary rays. It is uncertain whether meanwhile the non-parenchymatous elements of the wood also grow, as in the cortical bundles of Cycas (Sect. 195).

4. In the stem of *Phytolacca dioica* the *beginning* of the secondary thickening is naturally different from that in the roots. The first cambial ring appears normally in the primary ring composed of the bundles of the leaf-trace (comp. p. 249), together with intermediate bundles. The periphery of this, marked by the outer margins of the primary phloem-bundles, is immediately surrounded externally by some 2–3 layers of parenchyma; further outwards there follows an almost closed ring of bast fibres, next to which is the large-celled parenchyma of the outer cortex. The ring of bast-fibres is to be regarded as the limit of the layer of primary bast. The layers of parenchyma just mentioned, which adjoin it internally, show for the future, at least for the most part, growth by dilatation like the outer cortex. But the parenchymatous cells, which succeed them internally, and which accordingly belong to the margin of the phloem-bundle, begin, when the increase derived from the first cambial ring has gone on for some time, to extend greatly in a radial direction, and to divide tangentially. These processes arise at certain not exactly defined points of the periphery, and extend laterally from them over medullary rays and bundles, so as to form an annular layer showing the above phenomena. As far as has been investigated, this is derived from only one, or at most here and there from two layers of cells. After several successive tangential divisions the division stops at the inner side of the layer in question, their products grow into parenchymatous cells much extended in a radial direction: these retain with considerable accuracy the arrangement in the radial series in which they arose. In the outer part of the annular zone the tangential division continues, the beginnings of corresponding groups of wood and bast, i. e. of vascular bundles, alternating with medullary rays, appear arranged in a ring, which, like the first, increases normally by means of a normal cambium. At the outer limit of this second outer ring there arises later, in the same way as it arose, a third ring, and a layer of parenchyma separating it from the second; the same process may repeat itself through higher orders of rings. In each ring the formative activity of the cambium ceases *almost* simultaneously with the appearance of the next outer ring. Thus arise the often described concentric rings of vascular bundles, separated from one another by broad zones of parenchyma, the number of which annually formed may rise in a strong branch or stem to six and more. The rings are in this case often still more incomplete and irregular than in the root of Beta.

Connecting bundles between the successive rings are found, according to Nägeli, only in the nodes.

Sect. 193. In the anomalies thus far described the increase in thickness sometimes takes place like the normal increase in centrifugal progression; neglecting possible pathological states, the growth of the tissue within the cambium, which is at the time active, is soon ended and disappears. Another condition was only casually indicated for many of the cases hitherto described. We must now return to these in connection with others.

There are a number of parenchymatous stems and roots in which the old parenchyma, far distant from the active cambium, has in all regions of the transverse section, not only the *power* of growth and formation of new tissue, which it puts forth when wounded and so on, but also in the uninjured plant it really grows continuously, increases the volume and number of its cells, and produces secondary meristem, from which strands of wood and bast, and cambium may be derived. Leaving on one side the phenomena in the Cycadeæ, Sect. 195, which do not strictly belong to this category, it has never been accurately investigated how far the mature non-parenchymatous elements follow this growth. As far as appearance goes, they seem usually to play a passive part.

A number of the most peculiar anomalies owe their origin to these phenomena of growth and secondary development.

From the first series, viz. the stems of Lianes, Crüger quotes a number of phenomena of this category, which require more exact investigation. Thus the zones of intermediate parenchyma between the old successive thickening layers of Securidaca volubilis are said to grow continuously broader, while room for this growth is provided by widening of the radial bands of parenchyma in the rings outside it. Crüger gives the same information for the Dilleniaceæ.

Much more extended processes of growth and secondary formation, which fundamentally alter the whole arrangement of the tissues and even the form of the stems, occur in the Bauhiniæ, many Malpighiaceæ, Urvillea, and Bignoniaceæ.

The originally regularly formed and continuous xylem is here split into pieces by growth, i.e. extension and cell division of the bands of pith and xylem-parenchyma: these pieces have an independent growth in thickness by means of a cambium surrounding them, which is in part undoubtedly a secondary formation, and which forms bast also on the side turned away from the wood. In addition to the repeated splitting of the already formed strands of wood, new ones with a further individual growth may be formed from secondary meristem.

The splitting of the wood, described above, pp. 574, 575, for certain genera of Bignoniaceæ, occurs e.g. in the simple and diagrammatic case of Anisostichus capreolata (Fig. 237), since, after being stationary for years, extension and division of parenchymatous cells begins in the pith, and, extending from the pith radially towards the four plates of bast, splits up the wood into its four main segments. The segments of wood, which have from the first been backward in increase in thickness, are split off from the adjoining main segments on both sides, or remain connected with one, according as the two broad medullary rays adjoining them, or only one of them, take part in the extension of parenchyma. Also the four bast-plates, or their parenchymatous portions, undergo a process of widening: but they are again narrowed, since the split off and superseded

segments of wood undergo considerable increase at their outer side, and are extended in a fan-like manner so as to grow into the bast-plates, and since fan-like excrescences grow out also from the lateral margins of the main segments of wood. Each excrescence of wood starts from a corresponding segment of cambium, that of the short superseded segments undoubtedly from the original segments of cambium, that of the lateral margins of the large segments from secondary cambium; a further though weak production of bast by the segment of cambium corresponds to each excrescence of wood. The process in A. capreolata has not, as it appears from other writers, been observed much further than here described and illustrated. But in other Bignoniæ[1] the splitting of the wood in the first instance goes further; it is broken up successively into numerous segments corresponding in general to its dichotomies: these are separated by radial bands of parenchyma, and surround a central portion, in the transverse section of which are seen numerous strands of wood of various form. It is uncertain how far the latter are of secondary origin, or are thrown off from the old wood by corresponding growth of parenchyma. That the latter is the mode of origin of some of them, and is provided for to a certain extent from the first, is shown to be probable by the islands of parenchyma, which lie near to the medullary sheath in the young still undivided xylem of Melloa populifolia (Fig. 226). In the old stem the xylem is cut up throughout by broad bands of parenchyma and bast, and especially a number of central bundles are separated from the peripheral ones.

FIG. 237.—Anisostichus capreolata (Bignonia L.). Transverse section through an old stem. Natural size. Compare the young stem, Fig. 224, p. 570. The four projecting segments of the xylem are completely split apart from one another to the middle, by extension of the pith and of the bast-plates. Three of the small superseded segments of wood lie also separately in the surrounding tissue, and are extended in a fan-like manner at the peripheral margin. Two of the four segments of wood are further radially split, in the case of the lower one to the left, as far as the pith. From the margins of the segments of wood numerous excrescences project in a fan-like shape into the plates of bast and parenchyma. Bast and parenchyma are shaded, the wood is left white, with the exception of an indication of annual rings and medullary rays. Externally the cortex is surrounded by fissured bark, which is drawn in black.

The separate segments of wood increase in thickness on all sides, either by segments of the original cambium surrounding them, or by secondary cambium; and it can hardly be doubted that the latter always forms new bast elements on the side opposite the wood. How great a confusion of segments of wood, and bands separating them, may arise by the growth described, and by successive splitting, is shown by Crüger's not very accurate figures of Bignonia Unguis[2], and by Fig. 238, reproduced from Schleiden's Grundzüge, which Crüger regards as the transverse section of an old stem of Bignonia, but Schleiden as a Bauhinia.

Similar phenomena of splitting and of independent further growth within the simultaneously growing parenchyma are shown by the originally more or less lobed xylem of climbing Malpighiaceæ[3]. Special generic peculiarities cannot at present be definitely laid down for this family. The splitting of the medullary sheath and of the rest of the wood by the growth of the masses of parenchyma, the independent growth in thickness of the separate segments of wood, which have no special pith of their own, have been already clearly described by Jussieu in this group, if it be overlooked that he often calls the growing intercalary parenchyma cortical tissue intruding (from the outside). In a living branch of Stigmaphyllum ciliatum 1^{cm} thick I have myself been able directly to follow the dilatation of the pith and of

[1] Compare Crüger, Botan. Zeitg. 1850, I. Taf. II.
[2] Botan. Zeitg. 1850, Taf. II.
[3] Compare A. de Jussieu, *l. c.*; Crüger, *l. c.*; and above, p. 577.

the radial bands of parenchyma of the highly parenchymatous wood, which extend from the pith, the consequent splitting and disrupture first of the medullary sheath, then of the outer regions of wood, the appearance of new cambial zones close to the separated segments of wood, which form also new bast, and finally also the appearance of new strands of wood and bast in the pith itself, which are derived from secondary meristem, and have an independent growth in thickness. The changes start, in the branch investigated, from a swollen portion twining round a wire and exposed to strong pressure, a fact which shows that they are at all events advanced by mechanical causes.

FIG. 238.—Bauhinia spec. Transverse section of a stem, two-thirds the natural size, from Schleiden's Grundzüge. *a* all dotted figures are portions of wood, sometimes with remarkably large pitted vessels; *c* bundles of wood, conspicuous by their whitish colour, with radial medullary rays, and arranged in a simple circle (probably the original narrow medullary sheath, split up). With exception of the circle (*c*) the rest of the wood consists for the most part of parenchyma, and the medullary rays take a sinuous course. The bands left white (*b*) between and around the woody bundles are masses of parenchyma and bast.

It is doubtless similar anatomical changes which bring about the frequent splitting up of the xylem in the old stems of climbing *Bauhinias*[1], especially of the section *Caulotretus*[2], of which the Fig. 238, which, according to Schleiden, is of a Bauhinia, may give an approximate representation. In these Lianes however there is, in addition to the phenomena in question, another also, which has not at all events been shown with certainty to occur in other forms, viz. a long continued *growth in length* of the old layers of wood, which may also be ascribed for the most part

[1] Compare Gaudichaud, *l. c.*, Tab. XVIII. Figs. 2, 3.

[2] [See v. Höhnel, Die Entstehung der welligflachen Zweige von Caulotretus, Pringsh. Jahrb. Bd. 13.—Also, Warburg, in Botan. Zeitg. 1883, p. 617, &c.]

to the parenchyma, and which must be the cause of the peculiar curling of the band-like stems or branches of these plants.

According to the known facts, which certainly require to be completed and tested, the following conditions, which in the strict sense only partly belong to this category, occur here.

The young internodes, with leaves in two rows, are bluntly four-angled. In transverse section the pith lies in the form of a cross, the arms of which are in the plane of the two orthostichies of leaves, and in one at right angles to it. It is surrounded by a normal woody ring (medullary sheath) consisting for the most part of relatively narrow and thick-walled, radially arranged elements, it is therefore dense: it is itself thicker between the arms of the cross-like pith than outside the latter, and therefore it is roundish or bluntly octagonal in transverse section. On this zone which scarcely attains a thickness of 1^{mm}, and sharply marked off from it, a softer wood is deposited by continued growth in thickness: it consists of wide pitted vessels, narrow hard sclerenchymatous fibres, and thin-walled, apparently non-lignified, fascicular parenchyma; these elements are variously distributed, according to the species, at least according to the specimens investigated, the names of which were for the most part not accurately determined; this need not here be described in detail. Numerous narrow medullary rays, and here and there single very broad ones, traverse the strands of wood, and are distinguished in the dry material by the brown contents of their cells. They are as usual placed with their peripheral ends perpendicular to the surface, and on the flat portions of the stem they are also curved near the middle in a curve convex towards the margins. The body of wood thus arranged now grows in thickness, especially at the two sides alternating with the orthostichies of leaves, so that the whole stem attains the form of a ribbon-like plate rounded off at the two margins. Perpendicular to the surface of the plate the increase of wood is generally of much less extent, so that over the pith the whole thickness of the stem is not greater, but often even less than at the sides. –

The thickening is usually stronger on one surface than on the other, so that the pith remains nearer the latter. Local inequalities of thickening lead in most, but not in all specimens at hand, to the formation of unequally thick and irregular longitudinal ridges and furrows. The cortex shows no generally remarkable peculiarities of structure, it is on the average of equal thickness round the stem, if the numerous local irregularities be not taken into account.

Older ribbon-shaped branches of Caulotretus, about $40–50^{mm}$ broad and 10^{mm} thick, show in their form the peculiarity that their margin is considerably shorter than the middle, the latter is therefore strongly undulated, and often in a direction very regularly perpendicular to the surface; the undulation is strongest in the middle around the pith, at the margin it is not present at all, and towards the latter it gradually diminishes[1]. Each crest and each hollow of a wave, i. e. each point of strongest curvature towards the two surfaces of the stem, corresponds to the insertion of a leaf, or axillary shoot; the latter is placed in the cases investigated somewhat higher (in acroscopic direction) than the last-named point. Young shoots, on the other hand, even those which are already flatly ribbon-shaped (e.g. one before me 10^{mm} broad and $3–4^{mm}$ thick) show no undulations, or have them hardly indicated at all; as they grow older the undulations become steeper.

According to these data the undulation must arise from the fact that with the successive growth in thickness either the margin of the plate becomes absolutely shorter, or the middle absolutely longer than at first. The former alternative is *a priori* improbable, and is not made more probable even by any direct observation. The other condition might, with reservation till exact quantitative measurements be made, be explained partially on the assumption that, as in many normally growing stems (p. 505), the elements of the successive zones of growth increase in length, but here to

[1] Compare the drawing in Duchartre, Elém. de Botanique, p. 166, Fig. 77.

a less extent at the margins of the plate than in the middle. This explanation, however, is not enough, since the successive elongation of the middle is greatest in the oldest zone surrounding the pith. The same holds as regards the attempted explanation made by Netto[1]. If the assumption of a shortening of the margins of the plate be excluded, the other alone remains, that in the old zones there is a continued growth in length; and since according to other data, known in the case of Angiospermous trees, such a growth in other elements, though not impossible, is less probable, while phenomena of growth may be proved to occur elsewhere in the older parenchyma, the anatomical basis of the elongation must first be sought for in the latter. For the proof of this assumption, and the demonstration of the anatomical changes which necessarily follow from it in the old zones, more accurate investigation is wanted, and especially measurements.

In old stems the swollen projections of the xylem increase in size, and the islands of parenchyma in width. The final splitting of the former into the pieces and lobes (Fig. 238) with independent growth can hardly come about otherwise than as above stated, but this point requires more exact investigation. The anomalies of structure are continued, according to Crüger, into the roots.

In the stems under consideration the whole parenchymatous tissue surrounding the isolated segments of wood, together with the periderm, follow their unequal growth for a long time by means of corresponding dilatation.

Especially in the Malpighiaceæ and the Bauhiniæ, however, the inequalities of growth, as the increase of thickness proceeds, are so great that the masses of tissue lying between the ligneous bodies are ruptured. At the surfaces of separation a formation of periderm takes place; perhaps also a throwing off of single bands of tissue as bark; this however has not been closely investigated. The stem now appears *split* into more or less numerous longitudinal strands, each of which is covered by a special cortex, coated with periderm; these are arranged in the most various manner parallel to one another, or are interwoven one with another, and separated for a distance and again united.

The above-mentioned behaviour of the stem of *Urvillea* lævis[2] belongs to this category, because in the second or third year the wood begins, as in the Malpighiaceæ, to become three-lobed. By growth in width of the parenchyma of the medullary rays the three segments of the wood corresponding to the three lobes are separated from one another, and each of them, with the adjoining third of the pith, is surrounded by a zone of cambium which thenceforth forms wood and bast, so that the stem contains three separately growing masses of wood and bast.

As less striking and fundamental internal secondary formations we may connect with the above those strands of wood which arise subsequently from secondary meristem, as described by Crüger, *l. c.*, in the pith of Doliocarpus, Argyreia, &c.; it is doubtful whether the masses of wood, which appear lobed in transverse section, and lie, as described by Oliver[3], enclosed in parenchyma in the stem of Acanthophyllum (of the family Caryophyllaceæ), belong to this category.

The formation of bast on the inner surface of old hollow stems of Carica Papaya should rather be included in the province of phenomena of pathological callus formation and regeneration.

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[1] Ann. sci. nat. 5 Sér. tom. VI. p. 317, &c.

[2] Radlkofer, Atti, *l. c.*, p. 63.—Gaudichaud, *l.c.*, Tab. XVIII. Fig. 20.

[3] Trans. Linn. Soc. London, Vol. XXII p. 289.

Sect. 194. On the other hand, the processes of growth and secondary formation in the old internal parenchyma of the wood, at a distance from the active normal ring of cambium, as seen in *fleshy roots*[1], belong to this class. They have already been described, p. 600, in Beta. Here they do not extend further than the growth of the parenchyma itself, and the dislocations of other tissues which result from it. New formations of secondary meristem and of cambium, and strands of wood and bast occur, however, as first shown by Trécul[2] in the old root of Myrrhis odorata, in the fleshy roots of Convolvulaceæ, and species of Rumex, according to the investigations of Schmitz[3], and according to Stahl[4] in the roots of Bryonia, and may be found more frequently in similar parts. Also the partial rings described in Sedum Telephium should be connected with the above; the spotted structure of thick Sumbul-roots may also find its explanation in the appearance of partial strands of wood in the old originally normal wood.

The roots of *Myrrhis odorata* always have at first the normal structure and secondary thickening, and they may retain this through life, and thus attain a great thickness. But, in most cases, after the normal thickening has continued for a long time, the formation by means of tangential divisions of radially seriate secondary meristem appears in the internal parenchyma of the wood at some distance from the middle: it begins from one point, and extends through an annular zone, which surrounds the root. This zone assumes the properties of an independent normal cambium, which, starting from its *outer* side, bordering on the peripheral wood, and proceeding inwards, that is in centrifugal succession, forms strands of bast of normal structure, alternating with medullary rays, and subsequently on the side remote from the bast layer, that is facing *outwards*, it forms strands of wood, which insert themselves exactly on the surrounding portions of the strands of wood, and increase in a centripetal, that is a reversed direction. This phenomenon is found in almost all roots 1^{cm} or more in thickness. According to Trécul a second internal layer of secondary meristem or cambium may appear in the same way as the first: this also, if I understand rightly, forms a new layer of bast in centrifugal succession. Finally, a new cambium, which also forms a layer of bast, may appear between the inverted strands of wood and those limiting them externally.

If this has happened, the root then consists of the following concentric layers: 1. Normal cortex with a layer of bast. 2. Normal cambium. 3. A layer of wood, placed normally. 4. A second internal cambium. 5. A layer of bast. 6. A layer of wood, placed normally. 7. A layer of bast. 8. A third internal cambium. 9. A layer of wood, inverted. 10. Cambium. 11. A layer of bast. 12. Axile strand of wood. This discovery of Trécul's may be only a special case of the various possible combinations of concentric zones of secondary formation. The zones that happen to be peripheral follow the internal secondary formation by dilatation, while the normal increase continues in the normal cambium. Further, any zone surrounding single strands of wood may form a cambial zone from secondary meristem, by means of which the single partial bundle undergoes an individual thickening, and becomes surrounded by bast.

In the roots and also many stems of *Convolvulaceæ*[5] investigated by Schmitz, various anomalies appear; viz. in the first place new strands of wood and bast, which grow by partial cambiums, and appear first in the parenchyma of the old xylem; secondly,

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[1] [Compare Weiss, Anat. u. Physiol fleischig verdickter Wurzeln. Flora, 1880.]

[2] Comptes rendus, 23 July and 6 Aug. 1866, tom. LXIII.

[3] Sitzsber. d. naturf. Ges. zu Halle, July 1874. Compare Botan. Zeitg. 1875, p. 677.

[4] By word of mouth.

[5] [Compare Dutailly, Sur quelques phénomènes dans les tiges et les racines des Dicotylédones, Paris, 1879.]

formations which arise in the cortex, and at first resemble the appearance of successively renewed cambiums (p. 590), though, as already intimated, they cannot always be included among these; and thirdly, combinations of the two processes.

In the old parenchyma of the root new partial cambiums appear, without the activity of the normal ring ceasing: they are partly in connection with normally-formed vascular bundles, partly with such bundles as have been formed from secondary meristem in the parenchyma separate from the former: in both cases they independently produce new secondary wood and bast in variable quantity, and with the normal succession and orientation. According as this takes place, the original tissue is displaced and crushed to such an extent, that finally the whole root may consist of irregularly grouped strands of wood and bast irregularly lobed in transverse section: each of these has its own ring of cambium. Still further disarrangement may arise by the original normal ring of cambium ceasing to be active, and becoming quite obscure; and by the appearance of repeated newly active layers of cambium in the partial xylem-bodies, as they did before in the original xylem. These phenomena appear in various individual forms, the description of which would here lead us too far, e. g. in the roots of Convolvulus Scammonia and Ipomœa Purga.

In very many roots of Convolvulaceæ, both in those which are perennial, and also quite regularly in the annual roots of Pharbitis hispida Choisy (Ipomœa purpurea), the other phenomenon appears: new strands forming wood and bast by means of their own cambium arise from secondary meristem, in the parenchyma of the secondary cortex, immediately outside the strands of bast. Their mode of origin is fundamentally the same as in the formation of renewed cambial rings at the periphery of old ones that are becoming extinct. The same process may also be renewed as in the latter case in successive zones lying further out. A difference however from the typical process of formation of renewed cambiums is found in the first place in the fact that the production on the part of the normal cambium does not cease with the appearance of the new bundles, but continues; and in the fact that, in most cases at least, closed cambial rings or segments of rings, producing strands of wood and bast alternating with medullary rays, and having a normal orientation, are not formed by the secondary development; but separate strands, each of which has its own more or less complete circular cambium, from which is derived an increase of wood and bast.

The whole transverse section thus resembles, to a certain extent, that of a stem of the Sapindaceæ: there is a central normal round xylem, surrounded by a number of smaller ones, in simple, later also in compound series. The longitudinal course of the peripheral strands is irregularly undulated; they are frequently connected laterally one with another, and with the normal xylem by anastomoses. The phenomenon described is found in the permanent stems of several species. Jussieu[1] describes in the case of C. malabaricus, in a stem 8^{cm} thick, 8–9 irregular concentric rings, and found the same in the stem of several undefined species. The same condition has long been known for the root of Ipomœa Turpethum, the roots of other species show the same, and in such a way that the cortical bundles appear only in the root, not in the stem. In the woody roots of the red garden Convolvulus (Pharb. hispida) they are well developed, but only pass up into the hypocotyledonary stem, and there pass over with thin ends into the strongly thickened normal xylem.

Both processes, the secondary formation of bundles in the parenchyma of the old wood and in the cortex, may be combined in the Turpeth root, and in the roots which are found in druggists' shops as Mechoacanna and Stipites Jalapæ. In these cases the secondary development of xylem-forming strands goes on, sometimes in the original normal xylem, while sometimes it may extend also to the xylem-bodies in the cortex.

As stated above[2], on p. 233, the massive starchy parenchyma of the napiform lateral

[1] *l.c.* p. 123.

[2] P.S. L. Koch (Verhandl. d. Naturhist. Vereins in Heidelberg, Bd. I. Heft. 4) has recently

roots of Sedum Telephium and its allies is traversed by vascular bundles, which are arranged in the transverse section in a ring. In many species, e. g. Sedum Fabaria, these bundles are connected throughout by a simple, normal cambial ring, which is but slightly productive. This is found sometimes also in S. Telephium, and even in certain roots of those stocks, which otherwise show the condition now to be described. This, which is the rule in S. Telephium, is as follows. At the point of insertion of the root a simple, normal, smooth, cambial ring connects the bundles; further between each pair of bundles the ring curves towards the swollen centre of the root, and the more deeply the nearer to the apex, till the stage is reached at which it is divided at the centre into as many separate partial rings as there were inflections or original vascular bundles. The separate rings are arranged in the transverse sections in a circle, and are separated one from another by bands of parenchyma. Each has a closed, and but slightly productive cambial layer, which both on the side next the wood and that next the bast forms especially parenchyma; on the side of the wood facing the middle of the partial ring are isolated small groups of vessels, on the side facing the bast, and corresponding to the latter, are those small groups of narrow elements of soft bast mentioned on p. 324. Towards the apex of the root the partial rings open, and unite again to form a normal xylem body of the root. Comp. Koch, *l. c.*

Sect. 195. The structure of the stem of the *Cycadeæ*[1] must here be dealt with generally, in connection with p. 256, since a separation of the primary arrangement from the various secondary changes could not be well carried out without too great sacrifice of clearness.

By way of making matters plain, it may be stated at once that the stem always has at first the same arrangement of tissues as that typical of the Dicotyledons and Gymnosperms; i. e. it has a normal ring of wood, bast, and cambium, which separates the outer cortex from the pith. The two last-named regions are always relatively strong; in the old stem of Cycas circinalis, investigated by Miquel, for instance, the outer cortex was more than 7^{cm} in thickness, and the thickness of the cylinder of pith 10^{cm}. They consist like the medullary rays of relatively thin-walled, permanently starchy parenchyma, and are traversed by the system of branched gum and mucilage canals, described above on p. 441. The cortex is covered by a superficial layer of periderm. The two kinds of leaves are, as is well known, arranged spirally, and are so close, one above another, that the fleshy scale-like expanded bases of the leaves are in superficial contact one with another. The numerous vascular bundles of the base of the leaf are united at the surface of insertion into two bundles of the trace, which enter the stem separately and symmetrically near the middle of the surface of insertion; they then diverge directly,

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shown that the ring of bundles now under consideration is nothing more than the very isolated vascular groups of a chiefly parenchymatous xylem of the root, which is derived from a typical radial root-bundle, the original elements of which had hitherto been overlooked in the massive parenchyma. The napiform roots of Sedum are thus a special case of very parenchymatous typical dicotyledonous roots. What is said above should accordingly be corrected.

[1] A. Brongniart, Rech. sur l'organisation de la tige des Cycadées; Ann. sci. nat. 1 sér. XVI. p. 369; Id. Archives du Muséum, I.—von Mohl. Ueber d. Bau d. Cycadeenstammes; Abh. d. Münchn. Acad. I. p. 397; Verm. Schriften, p. 195.—Miquel, Ueber d. Bau e. Stammes, &c. von Cycas circinalis; Linnæa, Bd. XVIII. p. 125.—Karsten, Organogr. d. Zamia muricata, in Abh. d. Berliner Acad. v. 1856, p. 193.—Mettenius, Beitr. z. Anat. d. Cycadeen; Abhandl. d. K. Sächs Ges. d. Wissensch. VII. p. 567.

the one to the right, the other to the left, and curving downwards through the cortex, they finally enter the bundle-ring, and there descend further in a radially perpendicular manner. This last part of their course, and their final lower insertion, has not been thoroughly investigated. The length of the curve, projected in the horizontal plane, and regarded as circular, which each bundle of the trace describes through the cortex before its entry into the ring of bundles, is not exactly defined, and appears not to be always the same, but has been estimated in the case of Cycas revoluta at least at 145° to 150°, but does not reach 180°, that is the coalescence of the two bundles. At the beginning of its course, as followed from the leaf-insertion downwards and inwards, each bundle passes for a long distance immediately below the surfaces of insertion of the leaves, that is just within the surface of the cortex of the stem, diverging but slightly from it, and running not exactly horizontally, but descending only slightly. In the last portion of its course, which is approximately equal in height to that of one leaf-insertion, it runs more steeply

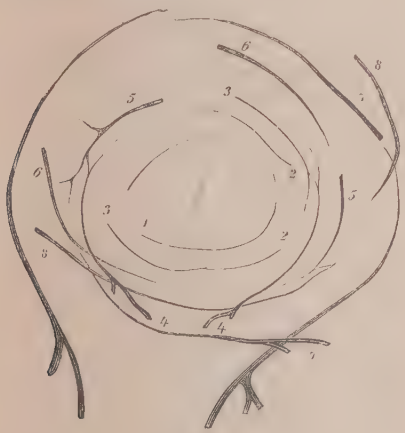

FIG 239.

FIG. 240.

FIG. 239.—Cycas revoluta. Course of the bundles of the leaf-trace, in a thick transverse section closely below the punctum vegetationis of a lateral shoot, made transparent with potash, and seen from its acroscopic surface; slightly magnified. The bundles, which run in different, but closely superposed planes, are drawn together in the plane of the paper, so that the point of exit is kept most dark, and each bundle is drawn from this point to that at which it curves steeply downwards; the bundles of the eight successive youngest leaves are successively numbered, 1, those of the youngest, highest, &c.; those of the oldest, 9, are not numbered. Between 4, 5, 7, and 8, radial connections are beginning.

FIG. 240.—Cycas revoluta. Transverse section with six bases of leaves, near to the apex of a small plant raised from a lateral bud; natural size. Parenchyma of pith, cortex, and leaves left white. The vascular bundles laid bare by the section are represented as lines, those cut transversely as dots. The inner circle is the still very narrow young ring of bundles surrounding the pith; it consists of the lower portions of bundles of the trace descending from above. Outside it are the delicate beginnings of the radial connections.

inwards and downwards, till it enters the ring of bundles. The condition described is accurately represented only while young. A thick transverse section through the shortly-conical end of the leafy stem, if made transparent, shows the leaf-traces of the youngest, uppermost leaves in the young cortex as simple symmetrical pairs of curves, which increase in width the further they are from the apex (Fig. 239). Closely below the conically diminished end, the stem and the ring of bundles assume a more or less cylindrical form; when, or even before the curves come, by means of the progressive longitudinal growth of the apex, to lie in the cylindrical region, the original arrangement is modified by the appearance of connecting branches. These are in the first place so directed as to follow the course of the curves them-

selves; along the periphery of the stem they connect the two curves belonging to one leaf on the side opposite the latter into a ring-like transverse *girdle*, open only at the two ends which enter the leaf: this girdle may frequently be closed even between the points of exit by a transverse anastomosis. Simultaneously with the connections described, anastomoses further appear in the second place between neighbouring girdles, their number and arrangement not being closely defined; others also appear, which run generally in a radial direction from the girdles, inwards and obliquely downwards, and insert themselves on the bundles of the primary bundle-ring. In Zamia muricata, according to Mettenius, these radial connections run unbranched and moderately straight from the ring of bundles to the girdles. In Cycas revoluta, Dion, and Encephalartos horridus they divide, as they pass from the bundle-ring, usually into two diverging branches, which branch further, and sometimes anastomose mutually with their branches, and sometimes pass on to the girdles. The whole of these branches form a complex and irregular cortical net-work of bundles (Fig. 240). In a specimen of Cycas revoluta Mettenius found that nine to eleven of the bundles or bundle-trunks that leave the ring belong to one leaf.

The average strength of the girdles, and of the radial connections and their branches, the special direction of their course, &c., show many variations, which cannot be enumerated here, partly according to species and individuals, partly, and especially in Dion, according as they belong to foliage or scale leaves. In strong stems of Cycas or Encephalartos the absolute thickness of the strongest reaches $\frac{1}{2}^{mm}$ and more. All the bundles of this original system, which may be called the *primary net-work of bundles*, are collateral; tracheæ and sieve-tubes are arranged between radial rows of parenchyma in radial rows, which are themselves interrupted by parenchyma; the tracheal elements at the medullary margin are often subsequently torn apart by the expansion of the parenchyma. All tracheal elements, as has already been noted on pp. 165 and 336, are tracheides; the innermost primordial tracheides are spirally thickened, the majority have transverse scalariform pits.

As far as is known the primary net-work of bundles is developed in its full complexity close below the end of the stem. The successive transverse portions of the stem undergo, it is true, a considerable growth in thickness after the moment when it is already completed, in the first place by the still continued expansion of the parenchyma of pith and cortex, and subsequently by the cambiogenetic increase to be described later. The primary net remains meanwhile permanent; both the radial connections, and especially the girdles, must therefore increase continuously in length. As Mettenius found, the spiral tracheides do not take part in this, they are torn apart and finally cannot be recognised. The scalariform tracheides grow, on the other hand, considerably in length; in the girdles of young leaves the shortest measured 0.09^{mm}; in those of older stems the length increased to $1{\cdot}4^{mm}$, in the oldest stems investigated to $4{\cdot}5^{mm}$. The unthickened points of the walls are thus expanded from the form of narrow transverse slits to broad elliptical pits.

In the primary ring of bundles a cambial zone arises, as far as is known, according to the normal mode for Dicotyledons and Gymnosperms, and this also produces wood and bast generally in the normal way. The strands of xylem and phloem are situated in the transverse section between broad multiseriate large me-

dullary rays, which form, when their longitudinal course is seen from without, acute meshes between the undulating bundles. Through these meshes all the leaf-traces and radial connections of the primary net-work of bundles pass between the secondary bundles, in their course from their internal points of insertion into the cortex. The parenchyma of the medullary rays, which surrounds them, consists of large radially elongated cells, which undergo only few tangential divisions as the thickening proceeds, so that one may almost speak of an interruption of the cambial layer by large-celled parenchyma at the points in question. It may be concluded even from these facts, and it is confirmed by further investigation, that the cambial zone arises in the lower ends of the bundles of the leaf-trace, which descend perpendicularly, and that the upper parts of them, which curve into the ring, take no part in its formation. Further it remains to be more exactly investigated, how far the radial connections share in the formation of the ring and cambium, and whether other intercalary bundles are formed in addition.

After it has once appeared the zone of cambium forms wood and bast in the normal way. Both retain a regular arrangement in radial rows, and both tracheæ and sieve-tubes are disposed in numerous narrow radial rows, consisting of one or more series, and interrupted by thin-walled parenchyma: these lie between relatively broad, but small, parenchymatous medullary rays. The tracheal elements of the secondary wood are exclusively tracheides of moderate width, and having on their radial walls several rows of transversely elongated bordered pits (Cycas, Encephalartos), or with a scalariform-reticulate wall (Zamia spec., Stangeria). The sieve-tubes have been treated of on p. 179. They are accompanied in Cycas, Dion, and Encephalartos by small groups of hard sclerenchymatous fibres, which are absent in Zamia and Stangeria; besides these Mettenius describes isolated chambered sacs containing klinorrhombic crystals.

The whole mass of secondary wood and bast has accordingly, in the main, the structure typical of sappy, parenchymatous stems of Dicotyledons. It remains always narrow in comparison with the pith and cortex; the bast is usually strongly developed relatively to the wood, and is often of equal thickness with it.

The investigated species of the genera *Zamia*, *Dion*, and also of *Stangeria*, show throughout their life the structure hitherto described, i. e. the primary network of bundles, and the normal ring of secondary thickening, which grows in thickness slowly and without limit. There are no other parts added to those described. But in the species of *Cycas* and *Encephalartos* the case is otherwise. Firstly, since in all of them the growth in thickness of the first normal ring is limited, it ceases after a time not exactly defined, but certainly longer than one period of vegetation, and is continued by a *renewed* cambial zone, which appears in the cortical parenchyma at the outer limit of the bast-layer—fundamentally in the manner described above in Sect. 191. The renewal of the ring may subsequently be repeated more than once. Miquel's large stem of Cycas, which was certainly many years old, had e. g. 6–8 successive rings.

Both the coarser structure of these rings and their histological composition are the same as in the first. Also the transit of the radial connections of the primary net through the medullary rays is conducted in the same way as in the former case. As in most cases of successively renewed rings, which were described in earlier

paragraphs, the rings are here also on the whole concentric, but with the same irregularities as have been repeatedly mentioned above. Usually the different segments of one ring are of unequal strength. Here and there the margin of a segment curves towards the next inner ring, and becomes continuous with it. The successive zones are therefore in direct connection, in not exactly defined longitudinal bands. The thickness which the successive rings attain decreases the further they are from the middle; they thus remain narrow in comparison with the cortex and pith. For instance, in Miquel's old stem, which has been repeatedly mentioned, the whole thickness of the 6–8 rings is hardly one-third of the radius of transverse section; the absolute thickness of the single rings varies between $0{\cdot}5^{cm}$ and $0{\cdot}2^{cm}$. A different relation is found at the inverted-conical base of stems which are derived from lateral buds. A piece of Cycas revoluta before me has, for instance, at the bottom a radius of transverse section of about 22^{mm}, of which 5^{mm} are referable to pith, five to the cortex, and twelve to the four almost equally strong rings of wood; 130^{mm} higher up in a radius of transverse section of 29^{mm}, 15^{mm} are referable to the pith, nine to the cortex, and only five to the two rings of wood, of which the outer is just beginning to appear.

Both the genera with successively renewed rings have, in the second place, in addition to those described a further system of accessory bundles, which is in *Cycas* a cortical system, in *Encephalartos* medullary.

The latter consists in the mature stem of numerous bundles distributed through the whole pith; these run in an undulating longitudinal course, and are connected one with another, and with the inner surface of the ring of wood by branches in all directions. They form an elaborate plexus, which is peculiar to the pith and gives off no branches into the cortex. According to Mettenius the bundles appear at a late stage, since they were not present in the whole upper half of a stem of E. horridus of the size of the fist, which he investigated. They may therefore, for the present, be ascribed to the category of cauline medullary bundles, which were described in other cases on p. 253. The medullary bundles are collateral; their xylem, according to Mettenius, never has spiral or annular tracheides, it has (according to incomplete investigation of E. Caffer) fundamentally the structure of the secondary strands of wood of the rings of the same plant, and seems to have a long continued, though very slow, growth in thickness. The stronger bundles in the stem of the last-named species are about 1^{mm} in thickness.

The accessory cortical system of *Cycas*, which Miquel found in C. circinalis, and Mettenius in C. revoluta, arises, according to the description of the latter, from strands of secondary meristem in the cortical parenchyma. Longitudinal rows of cells of the latter 'undergo a division into smaller cells, and become transformed into cambial strands, which gradually develope into small masses of wood.' It appears as though, as the stem grows old, new bundles of this order may be formed successively for a time; at least they were found in small numbers in young individuals, but in old ones in large numbers. Still this difference may be purely individual, and all the genetic conditions require still further investigation.

The arrangement of the bundles in the old stem investigated, in which they were numerous and strongly developed, is described by Mettenius in the main as follows. They are arranged in the transverse section in several irregular

annular zones. They take a sinuously curved course in a vertical direction, thus crossing the girdles and the radial connections. In an apical direction they may always be followed as far as the broad base of the foliage leaves. Here they are seated, and in all cases several of them of unequal strength, sometimes on the two shanks which pass out from the girdle into the leaf, sometimes on the first branchings of the latter in the base of the leaf itself, the strongest ones as a rule on the first branching. From this point of insertion they descend through the stem, and after a course of varying length they either unite, sometimes with similar ones from the same leaf-base, sometimes with others descending from above, or they insert themselves with their lower end, or with a lateral branch, on a girdle or on a radial connection. Free blind ends are not present; nor is there any connection with the bundle-system of lateral buds or roots.

The structure of the cortical bundles is such that their middle is occupied by a narrow parenchymatous prism of pith, and this is successively surrounded by a ring of wood and cambium, and a weak ring of bast. On the part of the cambium there is a permanent though slow increase, so that in old stems the thickness of the bundle rises from 2^{mm} to $5{\cdot}6^{mm}$. Wood and bast are traversed by thin-walled medullary rays, which are successively increased as the thickening goes on: between these the elements of the bundles are distributed as in the rings. The tracheides of the wood have usually a scalariform pitted thickening in C. revoluta, but few of them have bordered pits; spirally thickened ones are absent. At the points of insertion there is an alteration of the structure, inasmuch as the pith disappears; the elements of one bundle then become contiguous with the similar ones of the other.

The secondary thickening of the *Roots of the Cycadeæ*[1] which have been investigated always corresponds, at first, like the primary structure described on p. 357, with that of the typical roots of Dicotyledons and Gymnosperms, and especially with those which are fleshy and highly parenchymatous. The structure of the secondary elements of the bundle is fundamentally similar to that of the wood of the corresponding stem. For their individual characters and distribution, comp. Mettenius, *l. c.* For the investigated roots of Encephalartos (E. Caffer, longifolius) nothing of importance need be added to the above; at least, roots 3^{cm} thick showed no more remarkable phenomenon than very considerable extension of the internal parenchyma and consequent distortions of the strands of wood. Also, as far as the subject could be investigated, the primary outer cortex is in these plants thrown off at an early stage by periderm. While accordingly the roots described belong to category (2) of fleshy roots described on p. 516, that of Cycas revoluta must be placed in category (1) (*a*). The secondary thickening is in this case weak, the starchy parenchyma is still living in roots as thick as the finger, and is only covered on its outer surface by a layer of periderm. How long it persists is not known. As the root becomes older, according to Mettenius, the first cambial ring loses its activity, which is renewed by a peripheral cambium 'and the further growth proceeds exactly as in the stem.'

On the bushy dichotomous excrescences of the roots of Cycadeæ caused by their penetration by Nostoc, comp. Reinke, *l.c.*

[1] Mettenius, *l. c.*—van Tieghem, Reinke, *l. c.* See p. 356.

Sect. 196. The structure of the stem of *Welwitschia mirabilis*[1] is as wonderful as its form is peculiar. Moreover, by reason of the difficulty of preparation which the nature of old dry specimens presents, and of the lack of young fresh specimens, it remains still uninvestigated in many respects[2]. According to data at hand, which relate almost exclusively to the secondary thickening, it is connected in the matter of the arrangement of its tissues partly with many anomalous Dicotyledons, partly with certain Monocotyledons with secondary thickening, and in its histological structure with other Gnetaceæ.

The youngest plants, which are known, have a roundish stem, about the size of a nut, which is continued downwards into a strong tap root, provided with relatively small lateral branches. The round stem, called by Hooker the stock, has a convex uneven apical surface, the crown, on which, in the specimens examined, there is no trace of a true *punctum vegetationis* to be found. The blunt margin, by which the crown passes over into the lateral surface of the stem, is for the most part surrounded by the almost contiguous surfaces of insertion of two opposite, tongue-shaped leaves, which are regarded with good reason as the two persistent cotyledons; each of these leaves is inserted at the base of a deep ring-like furrow, which is so narrow that it is loosely filled up by the base of the leaf.

It is known that the plant retains this conformation throughout life, and suffers only this one important change of form, that the upper part of the stem grows continuously in width in centrifugal progression, so that it attains the form of an oblong two-flapped disk, in the blunt, more or less erect, marginal flaps of which are situated the foliar grooves. These together with the bases of the leaves increase in girth in proportion to the stem; the leaves themselves elongate throughout life at their base, and in a basipetal direction; the stem, crown, and root increase for many years in thickness, and attain colossal dimensions.

An anatomical investigation in the smallest specimens has not been undertaken, but in those which are hardly double their size, and successively in other older ones, this has been done. They all resemble one another, as far as investigations go, in the fundamental points of structure. The stem and tap root, with exception of the grooves of insertion of the leaves to be described below, are covered by a moderately thick, for the most part brown, fissured, bark-like, and very hard and brittle cortex. This envelopes a strong internal mass of tissue, which consists of vascular bundles, pale yellow thin-walled parenchyma, and those huge sclerenchymatous fibres described on p. 132, which are embedded in large numbers in the parenchyma of all sorts, and which point in all directions. As regards the vascular bundle-system, in the first place, in not too large specimens a large number of bundles are seen, which run with a radially converging course from the insertion of the leaf towards the lower end of the stem, or the upper part of the tap root. They are arranged in one plane, which lies between the surface of the crown and the outside of the stem, rather nearer the former than the latter; it has thus approximately

[1] J. D. Hooker, On Welwitschia, Trans. Linn. Society, London, Vol. XXIV.—Strasburger, Die Coniferen u. d. Gnetaceen, p. 374. [Bertrand, Ann. Sci. Nat. Sér. V. vol. XX.]

[2] [F. O. Bower, On the Germination and Histology of the seedling of Welwitschia mirabilis, Quart. Journ. Micr. Sci., vol. XXI. New series, June 1881.—On the further development of Welwitschia mirabilis, Quart Journ. Micr. Sci., vol. XXI, 1881.]

the form of a conical surface or of a disc, according to the inclination of the margins of the crown; in other words, the bundles form a middle layer in the stem, of similar form to the whole crown, and similar in direction to the surfaces of it. Hooker calls it the vascular stratum. It is, it is true, not directly proved, but hardly to be doubted, that the individual bundles are directly continuous into the leaves, we may therefore call it the *layer of the leaf-trace*. Examined more accurately, it consists of two layers of collateral bundles lying closely one above the other, and only separated by narrow bands of parenchyma: the bundles turn their phloem portions, which are strengthened by strong fibrous strands, towards one another, and their xylem portions respectively towards the crown and the outer surface of the stem. Connections between the two layers of bundles are probable, but not observed with certainty. The bundles of the individual layer are placed with considerable regularity side by side; they have an undulating course, and are, as far as can be made out, here and there laterally connected.

In the central portion of the stratum of the leaf-trace, between the middle of the crown and the insertion of the tap root, the course of the bundles is less regular, according to Hooker's description; here they form a tangled plexus, from which descend the bundles of the root, to be more accurately described below.

From the two layers of the stratum of the leaf-trace numerous much smaller bundles branch at all points: these run in an oblique direction, on the one hand towards the whole surface of the crown, on the other towards the outside of the stem, being curved in a sinuous manner apparently irregularly in all directions, and connected by branches one with another, thus forming a complex tangled net, which may be distinguished as the *peripheral network* of bundles. The bundles of the net which run towards the surface of the crown are often directly connected with those of the inflorescences.

The bundles, which descend into the tap root, are sometimes connected with those of the central portion of the stratum of the leaf-trace, sometimes with those of the peripheral net, as branches derived from them: the main direction of their course is, like that of the root, vertically downwards. In the transverse section of the root they are arranged with some regularity in concentric rings, separated from one another by zones without any bundles; these resemble the rings in stems of Menispermeæ and Gnetaceæ. The rings are moreover the more regular, and the bundles are larger the nearer they are to the middle. Hooker represents 5–7 such rings in transverse sections of thin roots; in a good young specimen before me, there are eight rings at a point close below the stem, and where the radius of transverse section was 30^{mm}: of these the outermost are very irregular, and the bundles small. The bundles of each ring have an undulating course, and often anastomose laterally; there are also frequent oblique connections between successive rings, especially the outer ones. The inmost ring surrounds, as a rule, a round pith-like central portion, apparently without any bundles, which is for instance in the specimen before me about 15^{mm} broad. When carefully examined, however, it is not entirely free from bundles, but contains a number of small strands of vessels, sieve-tubes, and fibres, the arrangement of which cannot be more exactly described because of the nature of the material. In some roots Hooker found in place of one inmost ring two eccentric rings side by side, round which the outer ones were arranged with considerable regularity, so as to form a simple system of rings.

All the vascular bundles above mentioned are, as far as investigated, fully formed collateral bundles, which are not in contact with active cambial layers; also the dissimilar tissue which surrounds them is fully developed. During the huge increase in mass of the whole plant the structure remains the same in its chief characters, the parts once present remain fundamentally unchanged, only similar new ones are added to them externally. This increase in thickness arises from a layer of cambium, which runs close under the cortex round the whole periphery of the body: it shows peculiarities to be mentioned below at the insertions of the leaves, and is least active at the middle of the crown of old specimens. It consists of a few layers of radially arranged cells, which are distinguished from the isodiametric cells of the adjoining parenchyma by their arrangement as described, and their thinner walls, the latter containing even here also the universally distributed granules of oxalate of lime; their radial is about half as great as their tangential diameter, or their height. Fresh young divisions may always be observed in 1–3 adjoining cells of one radial row, the initial layer in any case is thus only at most three layers of cells thick. The outermost vascular bundles adjoin the cambial layer, others, apparently older, are separated from it by layers of parenchyma, which are still radially arranged, but have begun to be displaced. If the description in the case of the Chenopodiaceæ, Amarantaceæ, and Mirabilis on p. 592 be called to mind, and the phenomena to be described in Chap. XVII in Monocotyledons, the data brought forward show that Welwitschia has an extrafascicular cambium, forming at its inside vascular bundles which anastomose in a radial and tangential direction, and alternate with interfascicular tissue. The whole intra-cambial body is wood in the sense of the word given on p. 591. Externally the cambium gives off a layer of bast consisting of parenchyma with scattered sclerenchymatous fibres, again coinciding with the type of Mirabilis and its allies. The production of this secondary cortex must be abundant; the living layer of cortex, which surrounds the cambium, is, it is true, but thin; for instance, in a transverse section before me of the upper part of the tap root it is sixteen parenchymatous cells in thickness; thick crusts of bark, thrown off by repeated internal formation of periderm, are superposed, as intimated above, on the older cortex.

Towards the margin of the stem and the leaf-groove the cortex becomes thinner, and the cambial layer less clear, since the whole tissue of the marginal portion, as far as the inner surface of the leaf-groove and the insertion of the leaf, with the exception of the thin outer cortical layer, consists of relatively delicate, regularly seriate cells, apparently still growing and dividing, thus resembling those of the cambium, between which lie sclerenchymatous fibres and small vascular bundles. On this delicate, half-meristematic tissue, if the term be allowed, is inserted the meristematic base of the leaf, which grows on in a basipetal direction. It may accordingly be said that the extrafascicular cambium passes gradually over into the half-meristematic tissue of the margin surrounding the leaf-groove: still it appeared as though even here a cambial layer could be distinguished at a certain distance from the surface. The doubt on this point must be dispelled by further investigations.

It is evident that the expansion of the margin throughout life is caused by the growth of the half-meristematic mass of tissue of which it consists. It is also clear that by means of it the bundles of the peripheral net running towards the margin

must suffer a marginal elongation, and that, especially also in the case of the bundles of the stratum of the leaf-trace, which always extend to the insertion of the leaf, a seat of intercalary growth must be situated in the latter, in which they undergo a permanent growth in length. Further, as the base of the leaf and margin of the stem increase in breadth, the number of vascular bundles lying side by side in it and in the stratum of the leaf-trace is increased; new ones must therefore arise successively in the latter, which apparently are connected as branches with those previously present. The mode in which these processes go on remains to be investigated.

If we start from the well-founded assumption that the mature Welwitschia plant, with the exception of the successively appearing flowering branches, is simply derived from the growth of the embryo known as Dicotyledonous, and retains throughout life its original conformation, the following may with all probability be stated, in accordance with the known anatomical facts, for the early stages of growth. From the broad surfaces of insertion of the Cotyledons a large number of original bundles of the trace converge towards the end of the root, which grows out to the tap root, and here unite into the axile bundle of the root. No bundles are added to the Cotyledonary trace from higher leaves, since there is no leaf-forming *punctum vegetationis* at all developed on the axis of the embryo. The ring-like 'margin' of the axis of the embryo, which bears the surfaces of insertion of the Cotyledons, increases together with the latter in breadth by permanent intercalary growth, proceeding in a centrifugal direction, so that the apex of the stem attains a discoid form; its tissue remains, with the exception of a thin cortical layer, permanently in a half-meristematic condition. The bundles of the leaf-trace undergo an intercalary growth in length at the insertion of the leaf, according as the marginal expansion progresses, and new ones are added to those first present; all those which are successively added arrange themselves in the double stratum of the leaf-trace. Simultaneously with the beginning of this phenomenon an extrafascicular cambium appears, in a manner which cannot be exactly stated, both round the whole stratum of the leaf-trace, and round the axile radial bundle, which is continued into the half-meristematic tissue of the margin, and remains permanently active in the whole remaining circumference of the stem and root as a distinct layer, producing secondary cortex in centripetal succession, and the secondary wood in centrifugal succession. The latter consists of the collateral vascular bundles, which alternate with the unlike tissue, maintaining the arrangement above described.

As regards the structure of the vascular bundles it may be added that they resemble closely those above described (p. 334) for the leaf, and are accompanied also, like them, by similar strands of fibres, but are not exactly similar to them in other points. Those of the stratum of the leaf-trace and of the inner circle of the root are, with their accompanying fibrous strands, much larger than those of the leaf, and have the form of narrow plates, the margins of which correspond to the outer and inner margins of the bundle. Their structure remains to be investigated in detail. According to Hooker's statements, irregularities in the course of the bundles, and also of the stratum of the leaf-trace, appear in old specimens. It is uncertain whether we have here to do with fresh intercalary formations in the parenchyma.

CHAPTER XVII.

SECONDARY THICKENING IN MONOCOTYLEDONS AND FERN-LIKE PLANTS.

Sect. 197. Most stems and roots of *Monocotyledons* show no secondary anatomical changes after the primary differentiation of tissue, with the exception of the formation of a superficial periderm, which often appears, especially in roots and rhizomes, but is by no means general. Comp. Sect. 24, and Fig. 168, p. 360. Its origin and properties are, as far as known, the same as described for the cortex of the Dicotyledons[1].

A cambiogenetic secondary thickening, forming wood and bast, is completely absent in the large majority even of tree-like stems of Monocotyledons and their roots. After the development of the primary bundle-cylinder the arrangement of tissues within the epidermis or layer of periderm undergoes no further change. It is true that there are statements and controversies upon the point that the internodes of such stems, e. g. of Palms, increase in girth for years after their first differentiation of tissue and extension, a phenomenon which, if true, depends upon an increase in volume of existing tissue-elements, not upon a cambiogenetic secondary formation.

Cambium and secondary wood and bast appear, as far as at present known, only in the more or less arborescent stems of Aloineæ (Aloe, Lomatophyllum, Yucca), of Beaucarnea, and the Dracæneæ (Dracæna, Cordyline, Aletris, &c.); in tubers of Dioscoreaceæ; species of Dioscorea, Tamus, Testudinaria; and the roots of Dracæneæ[2].

The primary arrangement of the above-named *stems* is according to the Palm type (p. 262). When it is at least so far advanced that all the primary vascular bundles have been begun, and are in course of development, the cambial layer appears: in a number of species, as Yucca aloifolia, Calodracon Jacquini, Aloe plicatilis, and Beaucarnea tuberculata, it appears immediately below the apex of the stem, even before the differentiation of tissues in the transverse section at that point is complete; in most Dracæneæ on the other hand—D. reflexa, marginata, Aletris fragrans—it appears in regions of the stem of considerable age, which have long

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[1] Compare Sanio, Pringsheim's Jahrb. II. p. 66.

[2] Treviranus, Physiol. I. p. 197.—Meneghini, Ricerche, *l. c.*; compare p. 263.—Unger, Dicotyledonenstamm (*l. c.*, compare p. 249), p. 46.—Schleiden, Grundzüge (3 Aufl.), II. p. 159.—Schacht, Lehrb. I. p. 329 et passim.—Nägeli, Beitr. I. p. 21.—Millardet, Anatomie, &c., des Yucca et Dracæna. Mém. Soc. des Sc. Nat. de Cherbourg, tom. XI.—Kauwenhoff, Bydr. tot de Kenntn. v. Dracæna Draco. Amsterd. 1864 (nach Wossidlo).—Wossidlo, Ueber Wachsth. u. Struct. d. Drachenbäume. Progr. Breslau, 1868 (see here the older literature).—Falkenberg, Vegetationsorg. d. Monocotyledonen. Stuttg. 1876.

been differentiated, and are situated 14–18 and 20cm, or many internodes below the slowly elongating apex. The initial layer of the cambium is a layer of parenchymatous cells characterised by no further peculiarities, which runs round the outer surface of the bundle-cylinder, and is thus extrafascicular. It is in close proximity to the outermost leaf-trace bundles, and must doubtless be regarded as belonging to the plerome-cylinder.

Radial growth of this layer and tangential divisions in reciprocal succession produce in centrifugal order secondary wood, in centripetal direction secondary cortex, in the same way and with similar arrangement to the extrafascicular cambiums described on p. 591, that is, *secondary vascular bundles* are formed, alternating with *interfascicular tissue*, which is always for the most part parenchymatous in the plants under consideration. Comp. Fig. 241. The true initial layer remains meanwhile always as a simple layer of cells. Its cells, as well as those produced from it, have the simple structure described on p. 465 for cambium and young secondary thickening. The form of both is that of erect rectangular prisms, which according to the individual case are 2–4 times as high as they are broad.

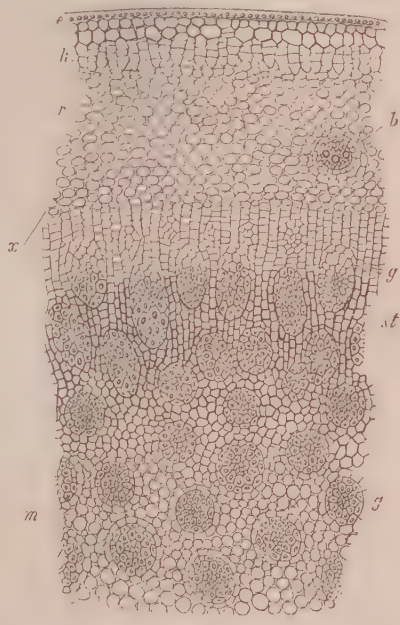

FIG. 241.—Piece of a transverse section of a stem of a Dracæna, probably D. reflexa, about 13mm thick and 1m high, slightly magnified. *e* epidermis, *h* pleroma, *r* primary cortex, *x* a bundle of the leaf-trace passing out through the latter; *g* primary bundles of the fibro-vascular system imbedded in parenchyma; *m*, a zone of secondary growth and conclusion with entire strands, further in its mature woody secondary vascular bundles, *st* interfascicular bands resembling medullary rays. From Sachs' Textbook.

Those sides of their rectangular bases, which are shorter in a degree which varies according to the stage of their development, are radially directed. In accordance with their mode of origin all the cells are arranged in radial rows. Those on the inner side of the initial layer develope on the one hand in centrifugal succession, and usually after one or more tangential divisions, into permanent interfascicular relatively wide parenchymatous cells. On the other hand, rapid longitudinal divisions facing in various directions appear at definite points in tissue-mother-cells, or longitudinal rows of them, separated internally from the cambium: from these are derived narrow-celled initial strands, which develope into secondary vascular bundles; the further development of the latter proceeds in centrifugal succession, while at the outer margin of the strand a formation of interfascicular parenchyma again begins. According to Millardet, one to three as seen in transverse section, or as many as nine and twelve original tissue-mother-cells, according to the size of the bundle, take part in the formation of an initial strand. When the number is large the cells concerned always belong to several radial rows. The arrangement and succession of the initial strands may be concluded from the arrangement of the vascular bundles to be

described below. During the development of the latter, as may be here remarked, there are extensions of the elements to many times the length of the cambial cells, while the transverse section remains the same or increases, and distortions and mutual displacements result, which have not been thoroughly studied in the cases before us, but a general opinion may be formed upon them from the points of view laid down in Sect. 137.

The secondary vascular bundles are directly connected, at least at the nodes, with the primary bundles of the leaf-trace, at the point where the latter curve outwards. They are connected one with another in their longitudinal course by numerous anastomoses both radially and tangentially, so that they form a net branched on all sides, the meshes of which are filled up by the interfascicular tissue. In the Aloineæ and Dracæneæ investigated, the meshes of the net are elongated, pointed and narrow, only as broad as a few interfascicular cells, and the bundles have a similar undulated course to that of the bundles in the Dicotyledonous stem, and the wood has a corresponding construction. In the stem of Beaucarnea, on the other hand, at least in the tuberous swollen base, the meshes are elongated and polygonal, attaining a width of over 1^{mm}, and forming a beautiful network, through which at the broad base of the stem the bundles belonging to the older roots of former years run in a radial direction. In radial longitudinal section and in transverse section the bundles in the two cases form more or less regular concentric zones. In the Dracæneæ these are irregularly pectinated, since the bundles of one alternate with those of the next inner zone, and project partially into the spaces between them; in the other investigated cases, however—Yucca, Aloe spec., Beaucarnea—they are more regular, and separated one from another by broad interfascicular spaces. The longitudinal course of the bundles diverges, as has been said above, from the vertical even in dense narrow-meshed woods. In the Dracænas, however, it is in the main perpendicular, if we neglect the undulations. In Yucca aloifolia, on the other hand, Millardet found the main direction, with many irregularities it is true, to be inclined strongly to the vertical, as much as 45°, and the direction of the inclination changes in successive layers; it is usually, but not constantly, directed to one side in each case for two successive zones, and in the two following zones to the opposite side.

The structure of the secondary vascular bundles is known in the Dracænas with some, but not with exhaustive accuracy. While the bundles of the leaf-trace have the collateral composition and the sheathing usual for Monocotyledons[1], and contain, according to Caspary[2], only tracheides, there being no vascular perforations even in the spiral primitive tracheides, the secondary strand is composed of a small phloem, which occupies about the middle of the bundle, and is surrounded by, on the average, 2–3 layers of tracheides. The phloem consists, as first pointed out by Wossidlo, of a small number of sieve-tubes with simple narrow-pored, callous transverse plates (p. 175); the tubes are accompanied by delicate cambiform cells. In transverse section the whole number of the thin-walled elements of the phloem is often very small, hardly as many as six, in other cases certainly larger: its general outline is accordingly very variable. At its periphery, that is, bordering on the tracheides, there are thick-walled cells, which have large round non-bordered pits on thin longitudinal walls. All the tracheides are, as far as known, of the same structure;

[1] Compare p. 322.

[2] *l. c.*, compare p. 165.

they are elongated, and spindle-shaped, with their pointed ends pushed between one another in various directions, and provided with oblique slit-like bordered pits (comp. p. 161) usually arranged in two irregular longitudinal rows on their very thick lignified walls. The peripheral ones adjoin the interfascicular parenchyma without any distinct sheath, and with sparsely pitted surfaces. The number of the tracheides of a transverse section of a bundle is moderate, it may be on the average according to the individual and species as high as 25–60. The form of the whole transverse section of a bundle is more or less broadly elliptical, with the longer axis placed radially; the relative breadth of the ellipse appears to be inversely proportional to the lateral distance of the bundles one from another, and the average distance seems to differ according to the species.

In the stems of Aloe and Beaucarnea the structure of the secondary bundles is, according to the data at hand, similar throughout to that described, but it has not yet been investigated with exactitude. The same holds, according to Millardet, for Yucca, with the limitation that the small strand of phloem does not lie in the middle, but at the outer margin of the bundle.

As has already been stated above, the interfascicular tissue is exclusively parenchyma in the species investigated, that is, not taking into account the crystal-containing sacs, which are scattered in it often in large numbers. Its cells retain on the whole their arrangement in radial rows, in which they passed off from the cambium, though they are often of necessity somewhat displaced around each vascular bundle. Their form also, and especially their height remains, on the whole, similar to that of the cambial cells. In radial direction they certainly undergo a more or less considerable expansion after the division which gave rise to them, so that their transverse section becomes almost quadratic—but rounded off owing to the formation of intercellular spaces; or it retains the form of a similarly rounded rectangle elongated in a radial direction. This expansion is often specially great in the rows running radially between the sides of closely-grouped bundles, so that in transverse section they resemble for a certain distance here and there the medullary rays with radially-elongated cells found in Dicotyledonous woods; this is very striking, e. g. in Aletris fragrans.

The structure of the interfascicular xylem-parenchyma shows nothing generally worthy of remark. In the hard woods of the Dracænas it is provided with rather thick lignified walls, covered with numerous round non-bordered pits, in the other investigated forms it remains thin-walled and sappy.

It is known that the secondary thickening described continues without limit, and that the old stems of many Dracænas attain a huge girth as the result of it. It is uncertain how far the necessary periodical remissions and accelerations of growth may lead to inequalities of structure in the wood, corresponding to the formation of annual rings of Dicotyledonous woods.

The secondary *formation of cortex*, which is derived from the cambium, is not very extensive, its product is thin-walled cortical parenchyma with crystal-containing sacs. Its cells after leaving the cambial layer undergo single transverse divisions; in Cordyline paniculata these are frequent, in other forms, such as Calodracon, Aloe sp., and Beaucarnea, they occur here and there; these cells thus become only half as high as the cambial cells. According to their origin they are at first always

arranged regularly in radial rows; it has not been accurately investigated how far this arrangement is disturbed by subsequent dilatation. Sooner or later there appears in the subepidermal layer the formation of the superficial periderm, already mentioned above; this continues through life, and follows the dilatation of the stem. In Beaucarnea it forms the thick masses of cork which are split up, as the plant grows old, from without inwards, and form a covering for the tuberous base of the stem.

Sect. 198. Most of the basal tubers of the Dioscoreaceæ require more exact investigation in all points. As far as known at present three categories of them may be distinguished: viz. (1) tuberous swollen roots—Dioscorea Batatas; (2) rhizomes with scaly leaves, and composed of many internodes—Dioscorea villosa; (3) leafless tubers, resulting from the swelling of the first epicotyledonary internode of the seedling—Tamus communis[1], also T. polycarpus[2], Testudinaria[3], and many species of Dioscorea. Only the tubers of category (3) have a cambium, and secondary thickening; and these resemble in the main phenomena those treated in the above paragraphs. The first origin of the cambium is unknown. In the specimens investigated it surrounds the whole lateral surface of the tuber inside a thin parenchymatous cortex: where the tuber is seated on the ground, as in Testudinaria, with a horizontal base, or, as in Dioscorea sinuata Hort., with an oblique flat base, it is absent towards the base. The form of its cells, the production of secondary wood and sparing cortex, the permanent arrangement in radial rows of the interfascicular elements, and the arrangement and connection of the secondary vascular bundles are fundamentally the same as in the stems described. The interfascicular tissue consists exclusively of thin-walled, starchy, parenchymatous cells often much extended in a radial direction, together with sacs containing raphides. This forms the main mass of the tuber. The thin secondary bundles, which form a net in the parenchyma, are collateral. Their xylem consists of elongated tracheides—at least I could not find vascular perforations—their lateral walls being reticulate or scalariform, or being for the most part closely covered with multiseriate, small, transverse, slit-like bordered pits; they are, especially in Tamus and Testudinaria, curved in the most various manner, and rolled one within another. The surface is covered at a very early stage with a periderm, which persists through life, and follows the dilatation, and which forms the usually sclerotic corky crust: it has already been mentioned, p. 113, that in Testudinaria the crust is fissured.

Sect. 199. A secondary thickening of *Monocotyledonous roots* is only known in the Dracænas, in Dr. Draco, marginata, fruticosa, reflexa[4], and in Aletris fragrans. While some of the roots of these plants retain the primary structure unaltered (p. 361), the pericambium of many stronger ones assumes the properties and functions of an extrafascicular cambium. As far as the few and incomplete investigations extend, the properties of these and their secondary products are exactly the same as those of the similar parts of the corresponding stem. As far as is known, the secondary thickening always begins first in the root, when it is of a considerable age, and when its primary tissue has long been fully formed, and its endodermal cells

[1] Dutrochet, Obs. sur les embryons végétaux. Nouvelles annales du Muséum d'Hist. Nat. IV. (1835), p. 169. [2] Compare Unger, Anat. u. Physiol., p. 239.

[3] Von Mohl, Ueber den Mittelstock von Tamus Elephantipes. Verm Schr. p. 186 (1836).

[4] Caspary, Pringsheim's Jahrb. I. p. 446.—Wossidlo, *l. c.* p. 27.

are specially thickened and sclerotic. Accordingly, the endodermis is split longitudinally by the growth in thickness, with the same phenomena as have been described for the splitting of cortical fibrous rings, p. 543. The primary outer cortex follows the growth in thickness, at least for a time, by means of growth by dilatation. It is uncertain whether it may be thrown off later by an internal formation of periderm.

Sect. 200. Among the *Fern-like plants* now living there are known, among secondary changes of tissue-distribution, some indications of formation of periderm, which have already been mentioned on p. 108. A secondary thickening, starting from a cambial layer, which produces secondary wood and secondary cortex, is only found in the Isoeteæ[1]. The phenomena in question, which there appear, differ in many points from those known in Phanerogams, but are to be connected with these as a very simple member of the series, which they themselves form. The single zones and parts related to the secondary thickening may without difficulty be compared with those of the Phanerogams, and may be designated by the same names without altering their meaning. Scruples, which have been felt against this, are allayed, if, in drawing the comparison, a start be not made from the normal Dicotyledons alone, but if the whole series of phenomena described in the above paragraphs be kept in view.

As is known from the descriptions[2], the short simple stem of the Isoeteæ is 2- or 3-lobed, in exceptional cases 4-lobed, and the lobes are separated from one another by longitudinal furrows, from which the roots arise. The middle of the stem is traversed longitudinally by the axile bundle containing tracheides, mentioned on pp. 280 and 347, which extends on the one hand to close below the meristematic group of the flat apex of the stem, and there developes further in an acropetal manner as a conical-cylindrical body, according as new leaves appear; on the other, basiscopic side it widens out into as many arms or wings as there are furrows in the stem. Each wing is opposite one furrow of the stem: its generally convex lower margin and its almost straight upper margin join into a single angle opposite the furrow. The wings increase in breadth as new roots arise, and the vascular bundles of the latter are inserted on them. The above data lead to the view put forward by Hofmeister and Sachs, that the whole axile bundle arises simply from the sympodial coalescence of the points of insertion, on the one hand of the bundles of the leaf-trace, on the other of the bundles of the roots.

The upper end of the tracheide-containing bundle, surmounted by the small group of apical meristem, is surrounded laterally by radial rows of meristem directed towards the surface, from which the thick parenchymatous primary cortex is derived: the latter retains the arrangement in radial rows. As far as a point close below the tracheide-bearing end, the bundle is surrounded by a layer of those tabular cells, which in I. lacustris are transparent, with lustrous walls; these have been above mentioned, p. 347, as probable representatives of the sieve-tubes. This layer has, like the bundle of tracheides, passed over into the permanent condition. While the

[1] [On the occurrence of a cambial ring in Botrychium, cf. Russow, Vergl. Unters. p. 119.]

[2] Von Mohl, Ueber den Bau des Stammes von Isoëtes lacustris. Verm. Schr. p. 122.—Hofmeister, Beitr. z. Kenntn. d. Gefässkryptog. I. Abhandl. d. Sächs. Ges. d. Wissensch. Bd. IV.—A. Braun, *l. c.*, compare p. 418.—Russow, Vergl. Unters. p. 139.—Hegelmaier, Botan. Zeitg. 1874, p. 481.—Compare also Sachs' Lehrb. p. 473 [2nd Eng. Ed. p. 483].

radial rows of meristem at the periphery also develope into parenchymatous cells, a layer immediately adjoining the tabular cells remains meristematic, and acts as cambium throughout life. This layer of cambium surrounds the whole axile bundle, with the exception of the apex, and the place where it is simultaneously perforated by the insertions of bundles from the leaf and root. It appears in the strict sense to be a single initial layer of cells, but this is not made out with certainty. The cells are of similar form to those of the tabular layer, but are on the average shorter in a radial direction, and are also similar in all points to those of the cambium of Monocotyledonous stems. Like these they show further successive radial extension, and reciprocal, tangential, longitudinal divisions. The products of the latter pass over on the side next the bundle in centrifugal succession, and on the side next the cortex in centripetal succession, into a definitive condition of tissue. In the relative extent of the thickening, however, in the two directions, there is this difference from all other known instances, that the axile bundle always remains thin and narrow in comparison with the cortex, and only increases in thickness by a few layers, while the secondary cortex grows in the course of years hundreds of times as much. The elements added in centrifugal succession to the axile bundle have the form of the tabular cells often mentioned. They retain the original radial arrangement and close connection one with another, and, at least in I. lacustris, are without intercellular spaces. Oblique divisions occur, deviating from the tangential longitudinal direction, and require more exact study. The cells retain for the most part in I. lacustris the above-described brilliant walls and transparent contents; the latter also require more exact investigation. Between the transparent cells there are isolated cells or longitudinal layers of them, which contain numerous starch grains. In terrestrial species, as I. hystrix, and Durieui, as Hegelmaier found, there is a regular alternation between transparent and starchy concentric layers, so that one layer of starchy cells lies between each series of 3–5 layers of transparent ones. Tracheides are entirely absent in most cases in the secondary thickening of the bundle; but they have been observed in single specimens of I. lacustris and Durieui, situated singly or in groups between the tabular elements, and resembling these in form and arrangement, but similar in structure to the original tracheides of the bundle. Finally, attention may be called to the fact that it is uncertain whether the above-mentioned first layer of tabular elements is the first product of the cambium, or belongs to the primary bundle.

The cambiogenetic secondary cortex consists exclusively of parenchyma, the cells of which contain according to the species large quantities of starch, or of starch and oil. According to their origin they remain arranged in radial and concentric rows; as they develope, wide air-containing spaces appear between the rounded corners, especially in species with an aqueous habit. Like the primary cortex the secondary thickening is also much more considerable between the furrows than opposite them. It is known that in each period of vegetation there is a large production of secondary cortex, which pushes the older parts of the cortex outwards, together with the old leaf-bases and roots which adhere to it, and with the vascular bundles belonging to these, which lie internally, and are stretched and finally torn away by the thickening; also that the old layers of cortex successively die and rot off, while their empty cell-walls turn brown; but they are not thrown off by a formation of periderm.

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